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New cave species of *Pectenoniscus* Andersson, 1960 (Isopoda: Oniscidea: Styloniscidae) and an identification key for the genus

Giovanna Monticelli Cardoso[1] orcid.org/0000-0003-2682-1643
Rafaela Bastos-Pereira[1] orcid.org/0000-0003-1344-1668
Leila Aparecida Souza[2] orcid.org/0000-0001-6757-9975
Rodrigo Lopes Ferreira[1] orcid.org/0000-0003-3288-4405

1 Universidade Federal de Lavras (UFLA), Centro de Estudos em Biologia Subterrânea, Departamento de Biologia, Programa de Pós-graduação em Ecologia Aplicada. Lavras, Minas Gerais, Brasil.
GMC E-mail: gmcardoso.bio@gmail.com
RBP E-mail: rafaelabastospereira@gmail.com
RLF E-mail: drops@ufla.b

2 Universidade Estadual do Ceará (UECE), Laboratório de Isopoda (LABISO). Fortaleza, Ceará, Brasil.
LAS E-mail: leila.souza@uece.br

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Abstract

The genus *Pectenoniscus* Andersson, 1960 currently presents two described species, one epigean, *Pectenoniscus angulatus* Andersson, 1960, from Nova Teutônia municipality, Santa Catarina state (Southern Brazil) and the hypogean *Pectenoniscus liliae* Campo-Filho, Bichuette and Taiti, 2019, found in two caves in the Serra do Ramalho karst area (Carinhanha municipality), Bahia state (northeastern Brazil). Recent surveys in karstic areas of Minas Gerais and Bahia revealed six new cave species from this genus, which are herein described. Two species occur in Minas Gerais state in the transition between the biomes Cerrado (Brazilian savannah) and Caatinga (mesophytic and xeromorphic forests): *Pectenoniscus montalvaniensis* n. sp. from Abrigo da Ema cave (Montalvânia municipality) and *Pectenoniscus juveniliensis* n. sp. from Gruta do Tabuleirinho cave (Juvenilia municipality). The other four species were found in Bahia state, in Caatinga biome: *Pectenoniscus iuiuensis* n. sp. from Baixa da Fortuna cave (Iuiu municipality); *Pectenoniscus carinhanhensis* n. sp. from three caves in Serra do Ramalho (Carinhanha municipality); *Pectenoniscus santanensis* n. sp. from Gruta do Padre cave (Santana municipality); and *Pectenoniscus morrensis* n. sp. from Gruta dos Brejões cave (Morro do Chapéu municipality). Aside from the taxonomic descriptions, we provide ecological notes for each described species, as well as an identification key for *Pectenoniscus*.

Keywords

Caatinga biome, cavernicolous species, Cerrado biome, Neotropics, woodlice

Corresponding Author
Giovanna Monticelli Cardoso
gmcardoso.bio@gmail.com

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Introduction

At present, the family Styloniscidae includes 16 genera, from which five can be found in Brazil: *Pectenoniscus* Andersson, 1960; *Cylindroniscus* Arcangeli, 1929; *Spelunconiscus* Campos-Filho, Araújo and Taiti, 2014; *Xangoniscus* Campos-Filho, Araújo and Taiti, 2014 (Styloniscinae); and *Iuiuniscus* Souza, Ferreira and Senna, 2015 (Iuiuniscinae) (Boyko *et al.*, 2008; Campos-Filho *et al.*, 2014; 2017; 2019; Souza *et al.*, 2015; Taiti and Montesanto, 2020).

Currently, the genus *Pectenoniscus*, erected by Andersson (1960), is composed of two species. The type-species, *Pectenoniscus angulatus* Andersson, 1960 is an epigean isopod found under stones in Nova Teutônia municipality, Santa Catarina state (southern Brazil) and is described as a small species with no eyes and no pigment. The second species, *Pectenoniscus liliae* Campo-Filho, Bichuette and Taiti, 2019, was found in two caves from Serra do Ramalho karst area in Bahia state (northeastern Brazil), which was considered troglobitic.

In the last twelve years, an intensification of biospeleological surveys has occurred in Brazil due to modifications in the laws guiding the conservation of the speleological heritage of this country. Such improvement of surveys has been culminating in the discovery of several new taxa, revealing a rich troglomorphic fauna, including terrestrial and amphibious isopods (Fernandes *et al.*, 2019). In this work, six new species of *Pectenoniscus* are described from caves in Minas Gerais and Bahia states in the biomes Cerrado and Caatinga, along with additional information about their habitats and an identification key for the genus.

Material and Methods

Field expeditions carried out by the Center for Studies on Subterranean Biology (CEBS) of Federal University of Lavras (UFLA, Lavras, Brazil) from 2012 to 2019 made it possible to collect several specimens discussed herein. The new species were collected with the aid of brushes and fixed in 70% ethanol. Specimens were measured and photographed with a ZEISS Axio ZoomV16 stereomicroscope coupled with an Axio Cam 506 Color camera. The appendages were dissected and mounted as micro-preparations in Hoyer's medium. The illustrations were obtained with the aid of a camera lucida mounted on a stereomicroscope (Leica DM750). The final illustrations were made with the software GIMP (v. 2.8) (Montesanto, 2015; 2016). The scanning electron microscope (Hitachi TM4000) was used for the observation of the dorsal ultrastructures. The type-material is deposited in the Subterranean Invertebrate Collection of Lavras (ISLA, UFLA).

Systematics

Family Styloniscidae Vandel, 1952

Genus *Pectenoniscus* Andersson, 1960

Pectenoniscus montalvaniensis n. sp.

(Figs. 1–4, 21, 22A)

Zoobank: urn:lsid:zoobank.org:act:E4E34FDD-8225-4F0A-A863-F90691934E57

Type material. Holotype: male (ISLA 77524), Brazil, Minas Gerais, Montalvânia, Abrigo da Ema (WGS84 -14.286846° -44.392976°), 25 November 2016, leg. R.L. Ferreira. Paratypes: 2 males, 19 females (ISLA 77525); 3 males, 6 females (ISLA 77526), same data as holotype.

Diagnosis. Triangular shape of antennal lobes; male pleopod 1 exopod triangular; pleopod 2 exopod trapezoidal, and pleopod 2 endopod apex with lobe directed inward and subapical denticles projected outward.

Description. Maximum length: male, 2.5 mm. Colorless, eyes absent (Figs. 1A, 3A, 4C). Dorsal scale-setae tricorn-shaped (Fig. 3B, C). Dorsal granulations disposed randomly on cephalon, in three rows on pereonite 1, two rows on pereonites 2–7 (Figs. 1A, 3A–C), smooth pleon (Fig. 3D). Cephalon with triangular antennal lobes obliquely directed and grooved dorsally; supra-antennal line bent in middle (Fig. 3A). Pereonite 1 with margin projected forward, not surpassing median portion of cephalon; pereonites 3–7 posterior margin progressively more concave; pleonites 3–5 epimera posterior points developed pleon narrower than pereon (Fig. 1A).

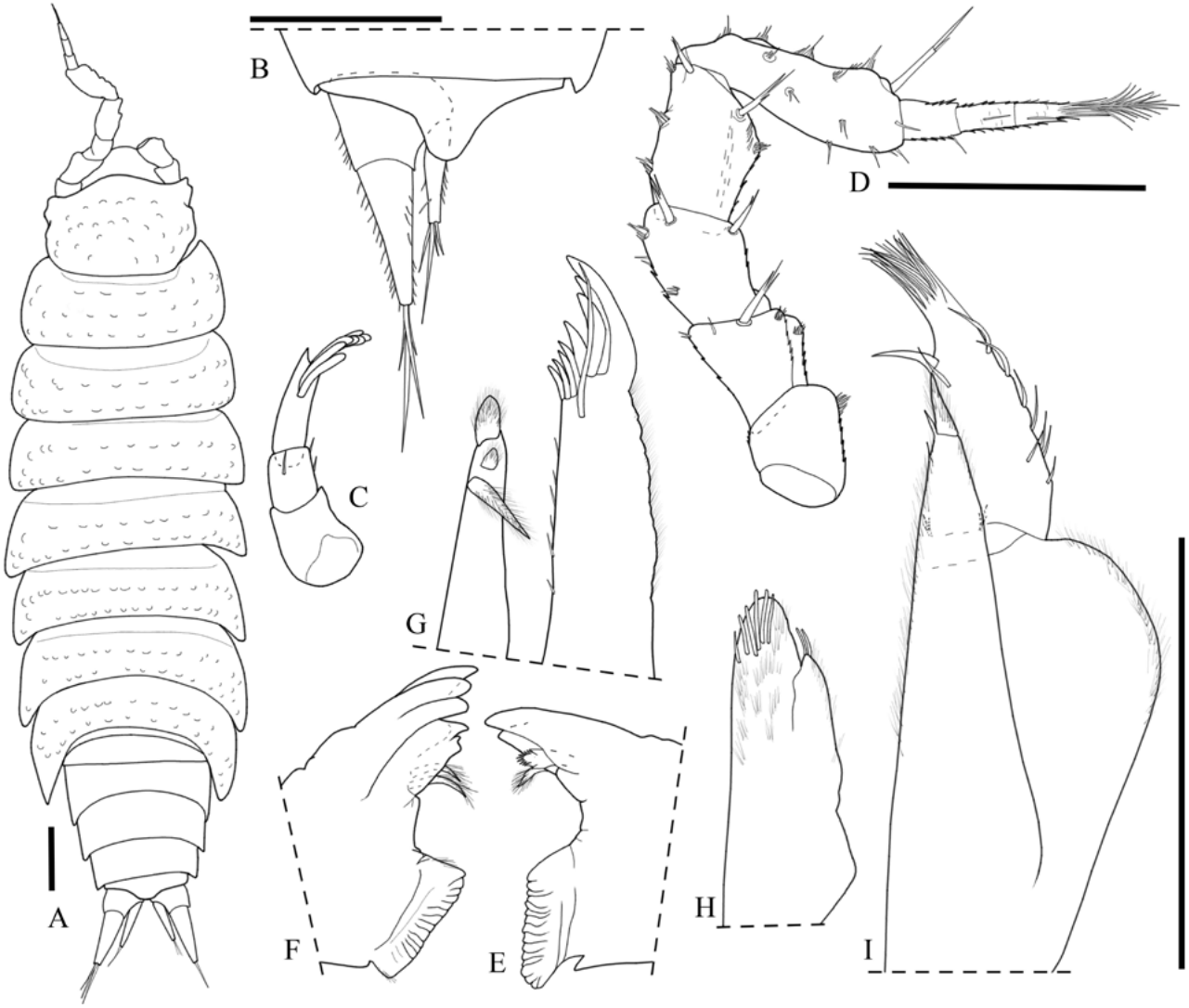

Figure 1. *Pectenoniscus montalvaniensis* n. sp. Male paratype: **A**, habitus, dorsal view; **B**, pleotelson and uropod, dorsal view; **C**, antennula; **D**, antenna; **E**, left mandible; **F**, right mandible; **G**, maxillula; **H**, maxilla; **I**, maxilliped. Scale bars: 0.2 mm.

Pleotelson with concave sides and round apex (Figs. 1B, 3C). Antennula with three articles, distal article with eight aesthetascs (Fig. 1C). Antenna reaches pereonite 1 when extended backward, fifth article of peduncle shorter than flagellum with one seta longer than first flagellum article; flagellum with three articles (Fig. 1D). Left mandible with two penicils (Fig. 1E); right mandible with one penicil, *lacinia mobilis* leaf-shaped (Fig. 1F). Maxillula outer branch with 4+4 teeth, apically entire, and one plumose seta; inner branch with three penicils (Fig. 1G). Maxilla with bilobate apex, inner lobe wider than outer lobe with several setae on distal margin (Fig. 1H). Maxilliped basis enlarged on distal portion; palp with two setae; endite triangular, apex with one triangular penicil and one lateral spine (Fig. 1I). Pereopod 1 antennal grooming brush composed of serrated scale setae longitudinally on propodus and on sternal margin of carpus (Fig. 2A); dactylar seta bifid with thin setule. Uropod protopod longer than wide, longer than distal margin of pleotelson; exopod longer than endopod, inserted distally (Figs. 1B, 3C).

Figure 2. *Pectenoniscus montalvaniensis* n. sp. Male paratype: **A**, pereopod 1; **B**, pereopod 6; **C**, pereopod 7; **D**, genital papilla; **E**, pleopod 1; **F**, pleopod 2; **G**, pleopod 3 exopod; **H**, pleopod 4 exopod; **I**, pleopod 5 exopod. Scale bar: 0.2 mm.

Male: Pereopods 6 and 7 (Figs. 2B, C) propodus with tufts of setae on tergal margin; and water conducting system; pereopod 7 ischium with convex sternal margin (Figs. 2C, 3D). Genital papilla (Fig. 2D) enlarged on medial portion, apical portion narrow. Pleopod 1 (Fig. 2E) protopod rectangular, three times wider than long; exopod triangular, apex round, lateral margin straight; endopod twice longer than exopod. Pleopod 2 (Fig. 2F) protopod rectangular; exopod trapezoidal, wider than long; endopod with distal article almost three times longer than proximal article, apex with lobe directed inward and subapical denticles projected outward. Pleopod 3 exopod (Fig. 2G) trapezoidal; pleopod 4 exopod (Fig. 2H) rectangular, and pleopod 5 exopod (Fig. 2I) rectangular with dorsal lobe.

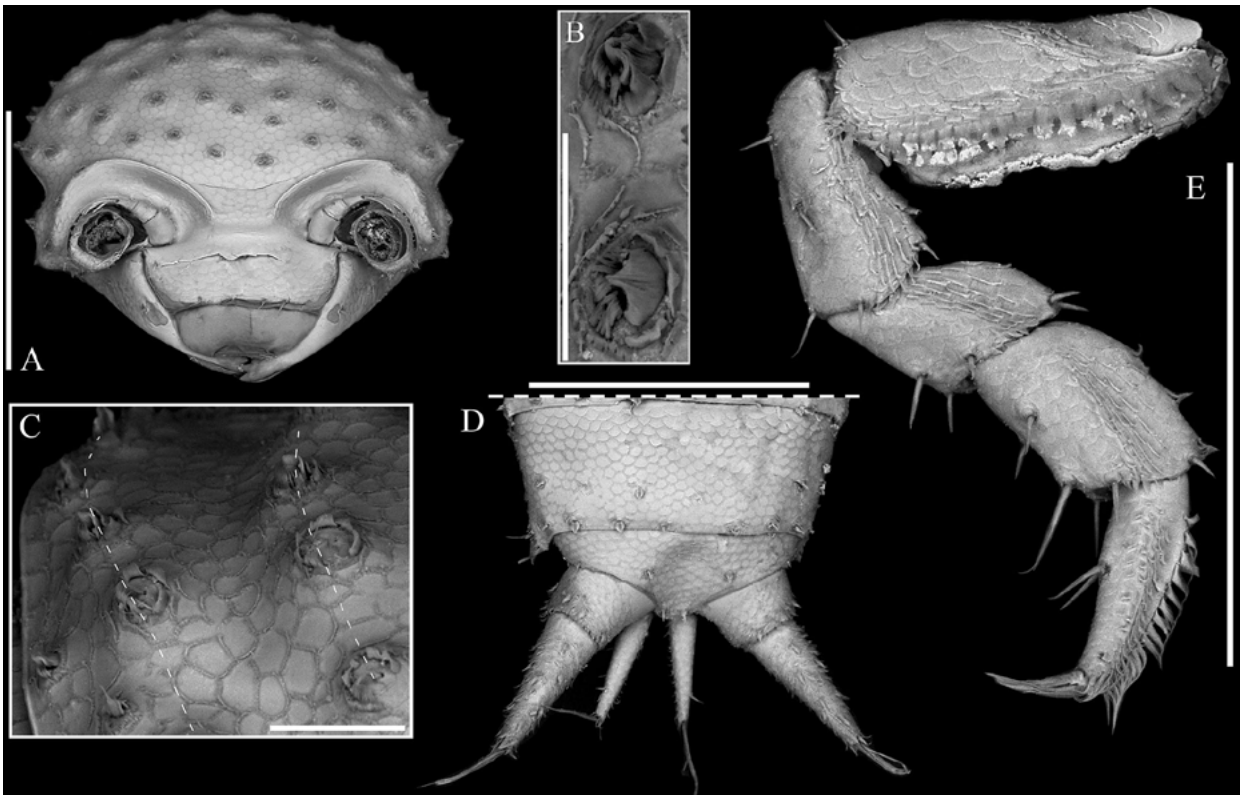

Figure 3. *Pectenoniscus montalvaniensis* n. sp. Male paratype: **A**, cephalon, frontal view; **B**, dorsal scaled setae; **C**, epimeron 2, dotted line indicating the lines of tubercles, dorsal view; **D**, pleonite 5, pleotelson and uropod, dorsal view; **D**, pereopod 7. Scale bars: **A, D, E**: 300μm; B: 40μm; **C**: 50μm.

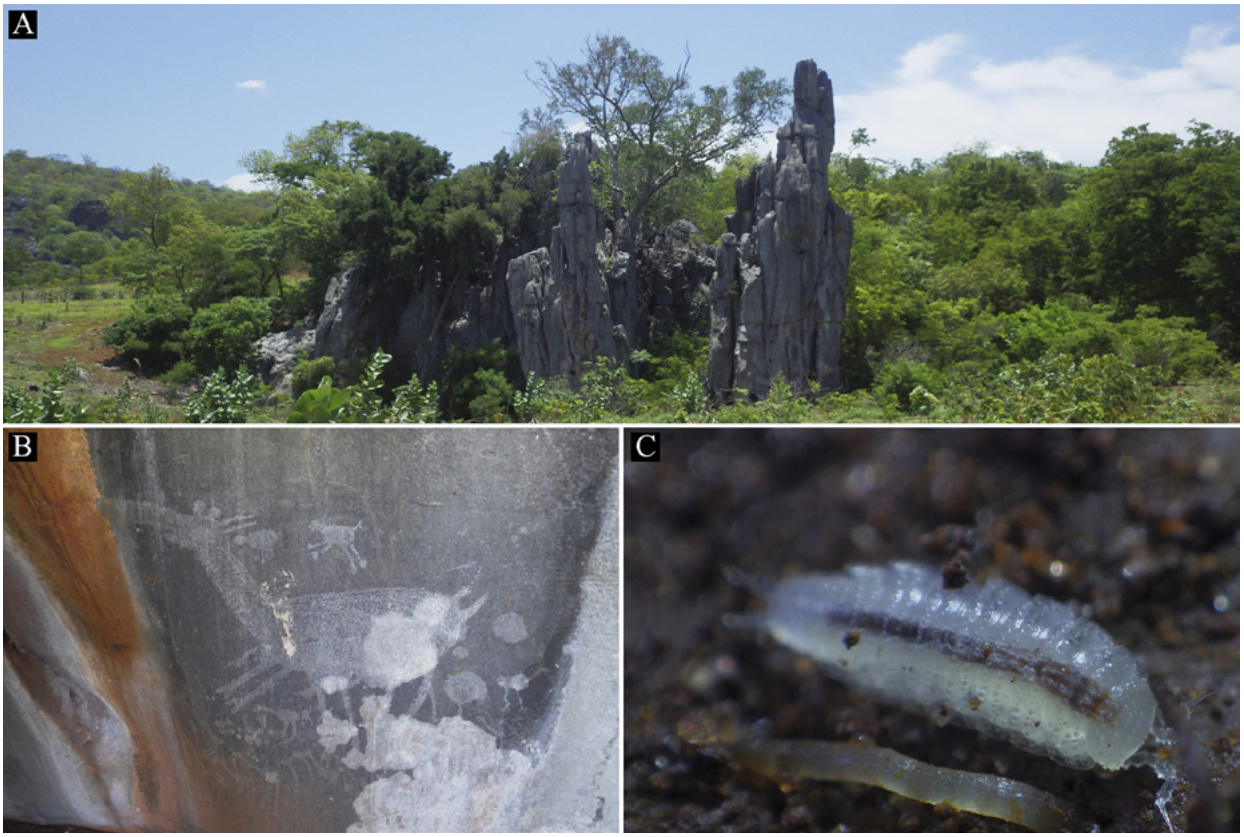

Figure 4. *Pectenoniscus montalvaniensis* n. sp. **A**, entrance of Abrigo da Ema cave, outside view; **B**, ancient rock engravings on the cave wall; **C**, specimen of *Pectenoniscus montalvaniensis* n. sp., approximately 2 mm.

Etymology. The specific epithet *montalvaniensis* refers to the city of Montalvânia, where the new species was collected.

Remarks. Pectenoniscus montalvaniensis n. sp. differs from *P. angulatus* by the number of articles in the antenna flagellum (3 *versus* 5 in *P. angulatus*), and by the shape of male pleopod 2 endopod (apex with lobe directed inwards *versus* apex with plate-like appendage in *P. angulatus*) and exopod (triangular *versus* rectangular in *P. angulatus*). In relation to *P. liliae, P. montalvaniensis* n. sp. differs by the triangular shape of antennal lobes (*versus* quadrangular in *P. liliae*), by the number of aesthetascs in the antennula distal article (8 *versus P. liliae*: 9) and the shape of male pleopod 2 endopod (apical portion chela-shaped with two triangular lobes in *P. liliae*) and exopod (ovoid in *P. liliae*).

Habitat and ecological remarks. Pectenoniscus montalvaniensis n. sp. was collected in a cave associated with an isolated limestone outcrop (Fig. 4A) in relation to the main massif occurring in the area. Although there are many caves in the region, only a few were sampled, suggesting that new populations of *P. montalvaniensis* n. sp. potentially can be discovered in the future in this region. The original name of the cave where this species was found (Abrigo da Ema - "Ema shelter" - in Portuguese) was attributed by archaeologists due to the ancient rock engravings on the cave wall (Fig. 4B). The cave presents aphotic conduits, the specimens were found concentrated on the cave floor (around 20 specimens), close to moist areas, where the humidity came from dripping speleothems. The main cave conduit seems to be trespassed by water flows during strong rains, which brings organic matter to the cave interior (especially vegetal debris). A few bat guano piles were observed in the cave, but no isopod specimens were found associated with them. Indeed, several individuals of *P. montalvaniensis* n. sp. were found close to roots, which were frequent on the cave floor (Fig. 4C). The dark gut content observed in the living specimens indicate they were feeding on dark brown organic debris, as plant material or eventually dead root masses. The external environment surrounding the cave is altered, especially by the replacement of native vegetation by pastures (Figs. 21, 22A). However, considering that this cave seems not to be frequently visited by humans, no direct impact for the species was detected.

***Pectenoniscus juveniliensis* n. sp.**

(Figs. 5–7, 21, 22B)

Zoobank: urn:lsid:zoobank.org:act:02D13338-26E0-410C-BE00-0D68F7831410

Type material. Holotype: male (ISLA 77527), Brazil, Minas Gerais, Juvenilia, Gruta do Tabuleirinho (also known as Lapa Grande) (WGS84, -14.37047° -44.288831°), 23 November 2016, leg. R.L. Ferreira. Paratypes: 6 females (ISLA 77528), 1 male (in slide) (ISLA 77512), 6 females (ISLA 77529), same data as holotype.

Diagnosis. Male pleopod 1 exopod triangular with acute apex; male pleopod 2 exopod triangular, and pleopod 2 endopod apex distal margin rounded with two subapical lobes on inner margin.

Description. Maximum length: male, 3.5 mm. Colorless, eyes absent (Figs. 5A, 7D). Dorsal scale-setae tricorn-shaped. Dorsal granulations disposed in two rows on pereonites 1 to 7, smooth pleon (Fig. 5B). Cephalon with round antennal lobes; supra-antennal line bent in middle (Fig. 5A). Pereonite 1 with margin projected forward, not surpassing median portion of cephalon; pereonites 3–7 posterior margin progressively more concave; pleonites 3–5 epimera posterior points developed; pleon narrower than pereon (Fig. 5B). Pleotelson with concave margin and round apex (Fig. 5B). Antennula with three articles, distal article with nine aesthetascs (Fig. 5C). Antenna reaches pereonite 2 when extended backward, fifth article of peduncle shorter than flagellum, with one seta longer than the first two flagellum articles; flagellum with three articles (Fig. 5D). Left mandible with two penicils (Fig. 5E); right mandible with one penicil, *lacinia mobilis* leaf-shaped (Fig. 5F). Maxillula outer branch with 5+4 teeth, apically entire, and one plumose stalk; inner branch with three penicils (Fig. 5G). Maxilla with bilobate apex, inner lobe wider than outer lobe with several setae on distal margin (Fig. 5H). Maxilliped basis enlarged on distal portion; palp with two setae; endite triangular, apex with one

triangular penicil and two small lateral spines (Fig. 5I). Pereopod 1 antennal grooming brush composed of serrated scale setae longitudinally on propodus and on sternal margin of carpus (Fig. 6A); dactylar seta bifid with thin setule. Uropod protopod rectangular, longer than distal margin of pleotelson; exopod longer than endopod, inserted distally (Fig. 6A).

Male: Pereopods 6 and 7 (Fig. 6B, C) propodus with tufts of setae on tergal margin, with water conducting system; pereopod 7 ischium with convex sternal margin. Genital papilla (Fig. 6D) medial part enlarged, apex narrow. Pleopod 1 (Fig. 6D) protopod rectangular, three times wider than long; exopod triangular with acute apex; endopod twice longer than exopod. Pleopod 2 (Fig. 6E) protopod rectangular; exopod triangular, twice wider than long; endopod with distal threefold longer than proximal article, apex distal margin rounded, without apical lobe; two subapical lobes on inner margin. Pleopod 3 exopod (Fig. 6F) trapezoidal. Pleopod 4 and 5 exopods (Fig. 6G, H) subquadrangular, bearing four-five setae on outer margin, exopod 5 with dorsal lobe.

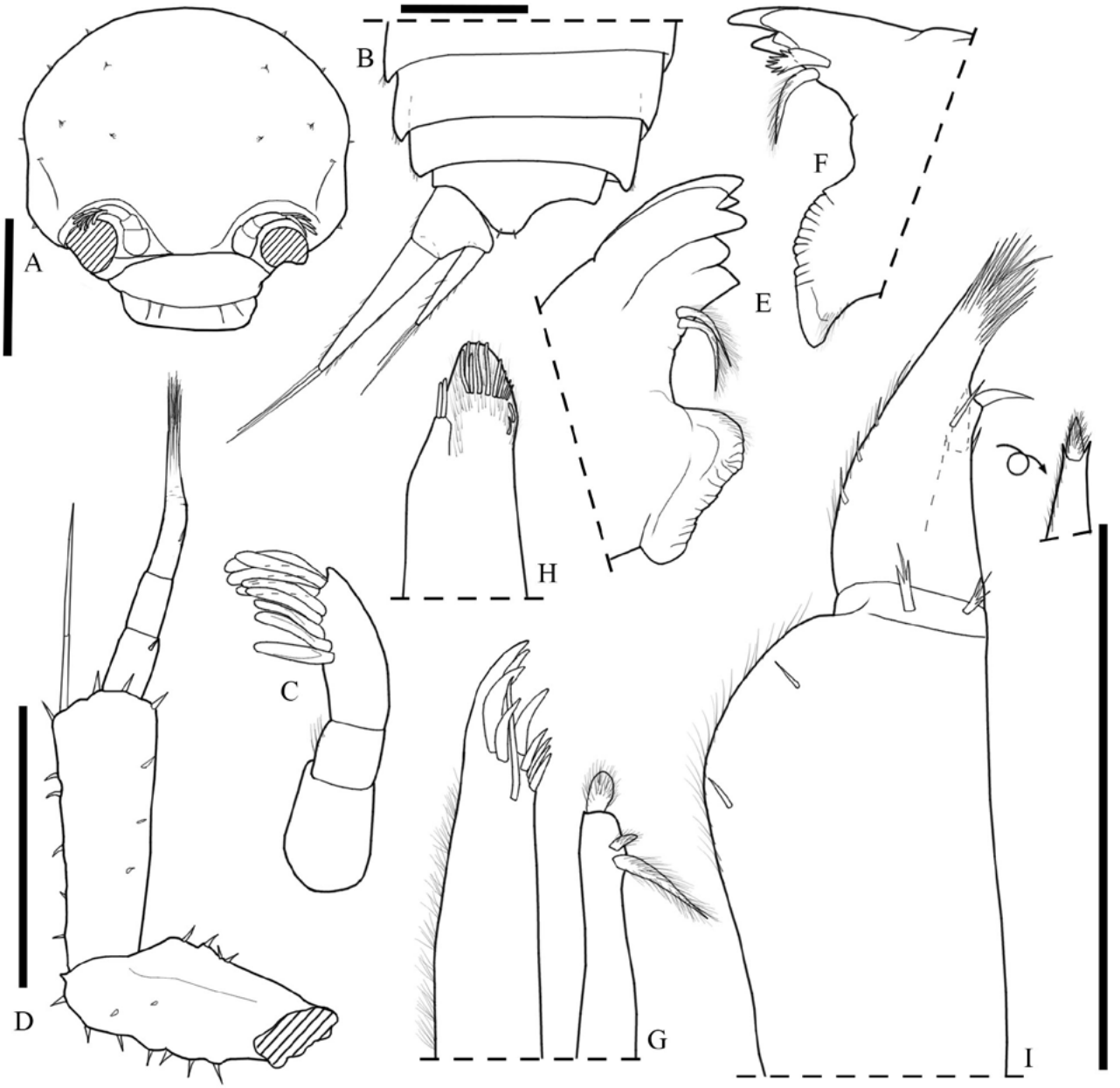

Figure 5. *Pectenoniscus juveniliensis* n. sp. Male paratype: **A**, cephalon, frontal view; **B**, pleotelson and uropod, dorsal view; **C**, antennula; **D**, antenna; **E**, left mandible; **F**, right mandible; **G**, maxillula; **H**, maxilla; **I**, maxilliped. Scale bars: 0.2 mm.

Figure 6. *Pectenoniscus juveniliensis* n. sp. Male paratype: **A**, pereopod 1; **B**, pereopod 6; **C**, pereopod 7; **D**, genital papilla and pleopod 1; **E**, pleopod 2; **F**, pleopod 3 exopod; **G**, pleopod 4 exopod; **H**, pleopod 5 exopod. Scale bars: 0.2 mm.

Etymology. The specific epithet *juveniliensis* refers to the municipality of Juvenilia, where the new species was collected.

Remarks. Pectenoniscus juveniliensis n. sp. differs from *P. angulatus* and *P. liliae* by the dorsal granulation pattern (two rows on all the pereonites *versus* three rows on the first pereonite and two on the others in *P. angulatus* and *P. liliae*), the shape of male pleopod 1 exopod (apex acute *versus* round in *P. angulatus* and *P. liliae*), and the shape of male pleopod 2 exopod (sub-triangular *versus* rectangular in *P. angulatus* and ovoid in *P. liliae*). Moreover, *P. juveniliensis* n. sp. differs from *P. montalvaniensis* n. sp. by the dorsal granulation pattern, by the number of aesthetascs on antennula (9 *versus* 8 in *P. montalvaniensis* n. sp.), by the shape of male pleopod 1 exopod with acute apex (*versus* round apex), by the shape of male pleopod 2 exopod with triangular shape (*versus* trapezoid) and by the male pleopod 2 endopod apex distal margin rounded, without apical lobe; two subapical lobes on inner margin (*versus* apex with lobe directed inward and subapical denticles projected outward).

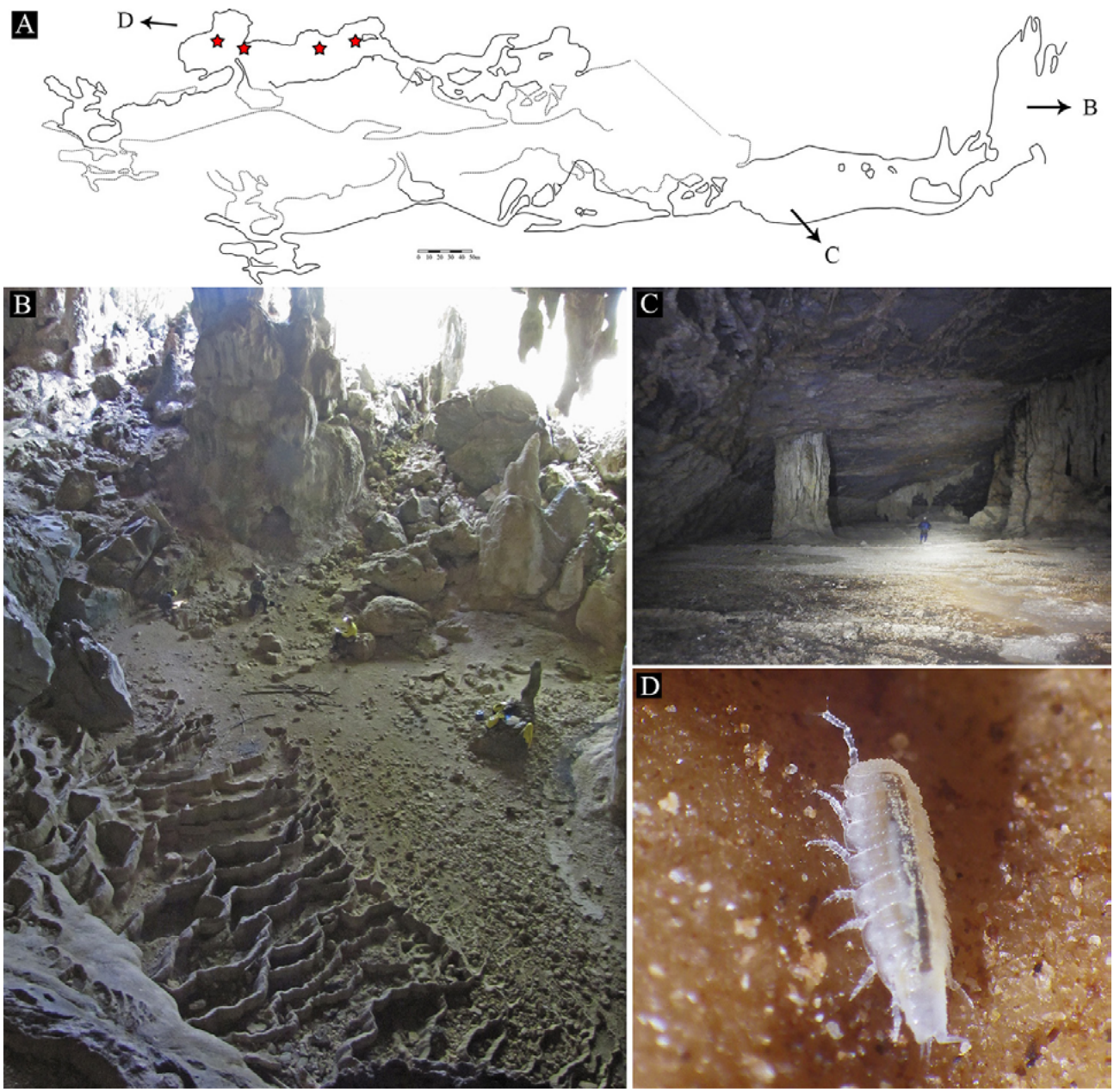

Figure 7. *Pectenoniscus juveniliensis* n. sp. **A**, cave map with collection sites; **B**, entrance of Gruta do Tabuleirinho, inside view; **C**, cave main hall; **D**, specimen of *Pectenoniscus juveniliensis* n. sp., approximately 3 mm.

Habitat and ecological remarks. Specimens of *P. juveniliensis* n. sp. were found in Gruta do Tabuleirinho (also regionally known as "Lapa Grande" cave), which comprises the biggest known cave in the municipality (Figs. 7A, 21, 22B). This cave presents a single large entrance (40 m high) (Fig. 7B). From the entrance onwards, the cave develops into a voluminous conduit (Fig. 7C), which is mostly dry. In this conduit, although several bat guano piles were observed, no specimens of *P. juveniliensis* n. sp. were found associated. Considering that the visit to the cave occurred in the rainy season, many travertine pools were filled with water, but no specimens were found in this conduit. Near the end of this main conduit, a lateral ascent leads to an upper chamber, which is moister and warmer than the lower part of the cave. Furthermore, it is extremely oligotrophic, and the organic debris consisted of rare and old bat guano piles. All specimens of *P. juveniliensis* n. sp. were found in this upper chamber, especially walking on moistened speleothems, as stalagmitic floors and flowstones (Fig. 7D). Despite the lack of visible organic

matter (bat guano), the dark gut content observed in the living specimens indicate they are feeding on some organic resources occurring in this upper level. Since this cave is voluminous, it is difficult to find specimens, however thorough searches have revealed that they are not rare along the cavity (we observed at least 20 individuals in a single visit to the cave). Furthermore, other specimens of *Pectenoniscus* were found in two other caves in the area (Gruta do Zé Prefeito and Gruta do Fóssil caves), however, only females were found, and since male characters are important to define the species, we choose not to assign them to the herein described species. Another described troglobitic species found in this cave is the unusual hydrometrid hemipteran *Spelaeometra gruta* (Polhemus and Ferreira, 2018). Gruta do Tabuleirinho cave presents obvious signs of human visitation, but currently only a few visitors have been entering the cave, according to local residents. Regarding the external landscape, it is composed of secondary forest under regeneration (close to the outcrop), and pastures (Fig. 22B).

Pectenoniscus iuiuensis n. sp.

(Figs. 8–10, 21, 22C)

Zoobank: urn:lsid:zoobank.org:act:2BF7FDE6-4BF8-4092-A726-CABF8E86E378

Type material. Holotype: male (ISLA 77530), Brazil, Bahia, Iuiu, Baixa da Fortuna cave (-14.547433° -43.654089°), 21 November 2016, leg. R.L. Ferreira. Paratypes: 2 males, 3 females (ISLA 77531), same data as holotype.

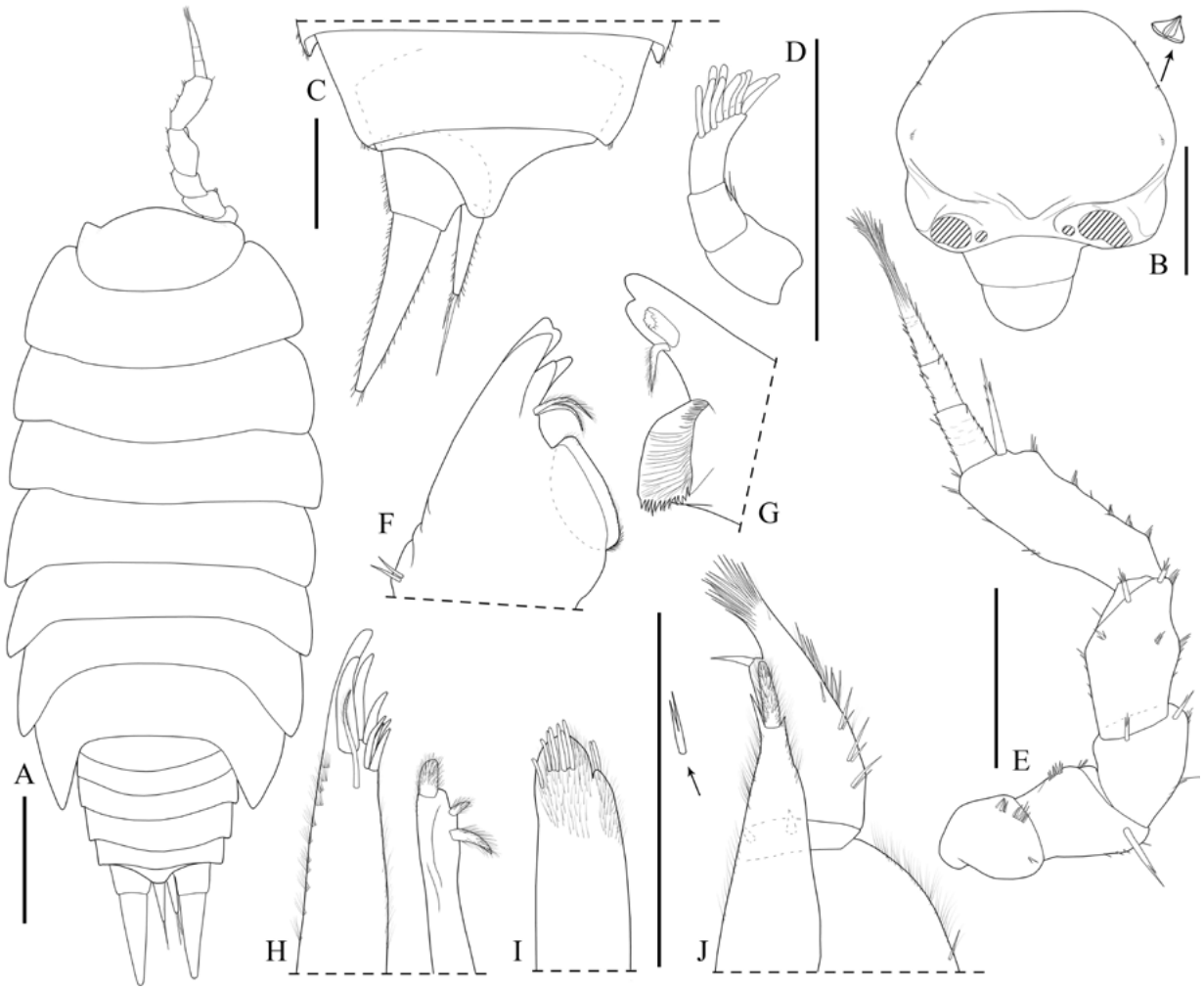

Figure 8. *Pectenoniscus iuiuensis* n. sp. Male paratype: **A**, habitus, dorsal view; **B**, cephalon, frontal view; **C**, pleonite 5, pleotelson and uropod, dorsal view; **D**, antennula; **E**, antenna; **F**, left mandible; **G**, right mandible; **H**, maxillula; **I**, maxilla; **J**, maxilliped. Scale bars: **A**: 0,5 mm; **B**–**J**: 0.2 mm.

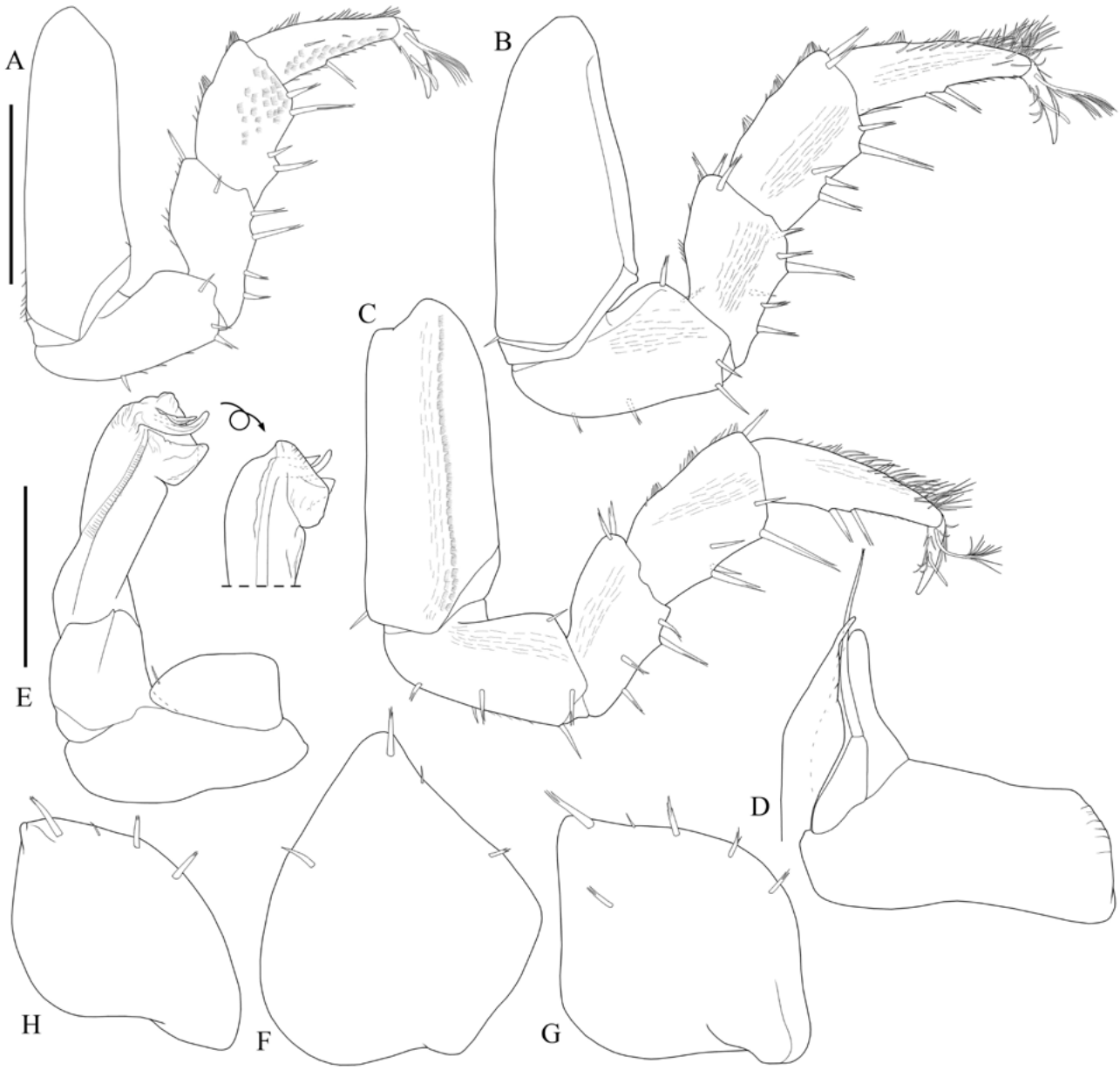

Figure 9. *Pectenoniscus iuiuensis* n. sp. Male paratype: **A**, pereopod 1; **B**, pereopod 6; **C**, pereopod 7; **D**, genital papilla and pleopod 1; **E**, pleopod 2; **F**, pleopod 3 exopod; **G**, pleopod 4 exopod; **H**, pleopod 5 exopod. Scale bars: 0.2 mm.

Diagnosis. Pereonites epimera well developed with pereonite 1 anterior margin projected forward; male pleopod 1 exopod triangular with lateral margin sinuous; male pleopod 2 exopod subrectangular, and male pleopod 2 endopod twisted with wrench-like shape and distal projection directed outward.

Description. Maximum length: male, 3 mm. Colorless, eyes absent (Figs. 8A, 10D). Dorsal scale-setae tricorn-shaped (Fig. 8B). Dorsal granulations disposed in three rows on pereonite 1 and in two on pereonites 2–7, smooth pleon (Fig. 8A, C). Cephalon with round antennal lobes; supra-antennal line bent in middle (Fig. 8B). Pereonites epimera well developed; pereonite 1 with anterior margin projected forward, reaching median portion of cephalon; pereonites 3–7 posterior margin progressively more concave, pereonite 7 distal margin reaches pleonite 3; pleonites 3–5 epimera posterior point developed; pleon narrower than pereon (Fig. 8A). Pleotelson with concave margin and round apex (Fig. 8C). Antennula with three articles, distal article with ten

aesthetascs (Fig. 8D). Antenna surpasses pereonite 1 when extended backward, fifth article of peduncle shorter than flagellum, with one seta longer than first flagellum article; flagellum with three articles (Fig. 8E). Left mandible with two penicils (Fig. 8F); right mandible with one penicil, *lacinia mobilis* leaf-shaped (Fig. 8G). Maxillula outer branch with 4+4 teeth, apically entire, and one plumose stalk; inner branch with three penicils (Fig. 8H). Maxilla with bilobate apex, inner lobe wider than outer lobe with several setae on distal margin (Fig. 8I). Maxilliped basis enlarged on distal portion; palp with two setae; endite triangular, apex with two spines and one penicil (Fig. 8J). Pereopod 1 antennal grooming brush composed of serrated scale setae on propodus and on sternal margin of carpus (Fig. 9A); dactylar seta bifid with thin setule. Uropod protopod rectangular, longer than distal margin of pleotelson; exopod longer than endopod, inserted distally (Fig. 8C).

Male: Pereopods 6 and 7 (Fig. 9B, C) propodus with tufts of setae on tergal margin; with water conducting system; pereopod 7 ischium with convex sternal margin. Genital papilla (Fig. 9D) medial part enlarged, apex narrow. Pleopod 1 (Fig. 9D) protopod rectangular; exopod triangular, long, with 2/3 of endopod length, lateral margin sinuous; endopod distal article twice longer than basal article. Pleopod 2 (Fig. 9E) protopod rectangular; exopod subrectangular, twice wider than long; endopod with distal article two times longer than proximal article, wrench-like shape, round apex with bifid distal projection directed outward. Pleopod 3–5 exopods (Fig. 9F–H) subquadrangular, bearing four-five setae on outer margin.

Etymology. The specific epithet *iuiuensis* refers to the mountain range where the new species was collected, Serra de Iuiú.

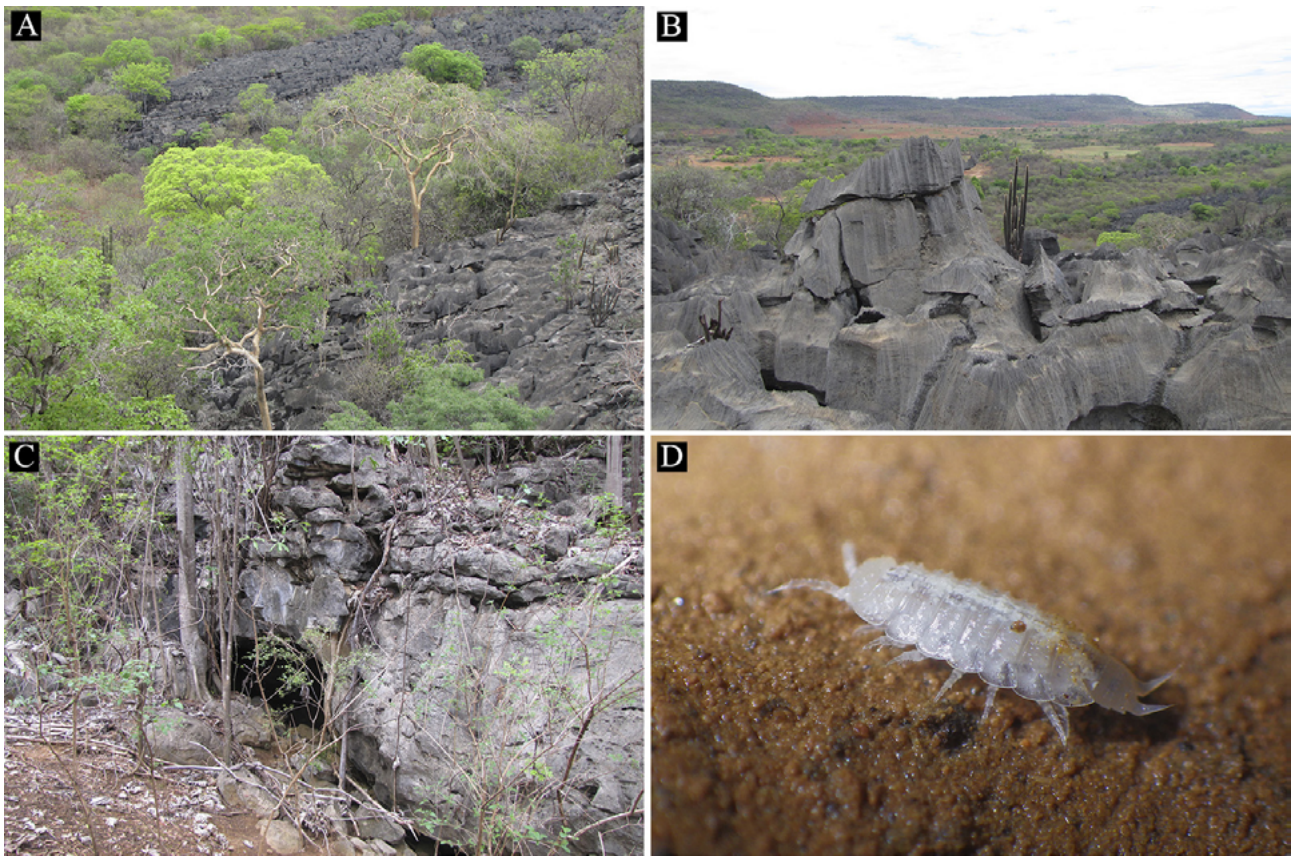

Figure 10. *Pectenoniscus iuiuensis* n. sp. **A**, surroundings of Baixa da Fortuna cave; **B**, landscape around Serra de Iuiú; **C**, entrance of Baixa da Fortuna cave; **D**, specimen of *Pectenoniscus iuiuensis* n. sp., approximately 3 mm.

Remarks. Pectenoniscus iuiuensis n. sp. differs from *P. angulatus* by the number of aesthetascs on antennula (10 *versus* 8 in *P. angulatus*), the number of articles in the antenna flagellum (3 *versus* 5 in *P. angulatus*), the shape of male pleopod 1 exopod (both with round apex, although lateral margin is sinuous *versus* straight in *P. angulatus*) and the shape of male pleopod 2 endopod. From *P. liliae*, *P. iuiuensis* n. sp. differs by the number of aesthetascs on antennula (10 *versus* 9 in *P. liliae*), the shape of male pleopod 1 exopod (lateral margin sinuous *versus* straight in *P. liliae*), the shape of male pleopod 2 exopod (subrectangular *versus* ovoid in *P. liliae*) and the shape of pleopod 2 endopod. From *P. montalvaniensis* n. sp. and *P. juveniliensis* n. sp., *P. iuiuensis* n. sp. differs by the well-developed epimera; by the number of aesthetascs on antennula (*versus* 8 and 9, respectively); the shape of male pleopod 1 exopod triangular with sinuous lateral margin (*versus* straight, in *P. montalvaniensis* and *P. juveniliensis*); and by the subrectangular male pleopod 2 (subrectangular *versus* trapezoid and triangular, respectively).

Habitat and ecological remarks. Specimens of *P. iuiuensis* n. sp. were found in Baixa da Fortuna cave (municipality of Iuiú, state of Bahia), which comprises a relatively small limestone cavity (Fig. 21). The cave is surrounded by vertical outcrops (Fig. 10A, B), requiring one to climb in order to reach the entrance (Fig. 10C). The single cave conduit presents a small autogenic drainage that arises in the innermost part of the cave (upstream) and flows toward the entrance, then sinking on the opposite side of the conduit (downstream) after the entrance. Hence, the cave entrance is laterally located in relation to this drainage. Individuals of *P. iuiuensis* n. sp. were observed walking on the cave sediments, especially close to the stream, always in the deeper portions of the cave. Few specimens were found despite efforts to make a thorough search in the cave due to its small dimensions. Another troglobitic species inhabiting this cave is the bochicid pseudoscorpion *Spelaeobochica iuiu* (Ratton *et al.*, 2012). The external area surrounding the cave presents a well-preserved forest (Figs. 10A, 22C), although pastures are observed a few kilometers from the cave (about 2 to 3 Km). No signs of human visitation were observed, probably due to the hard access to the cave; in this sense the cave is preserved.

***Pectenoniscus carinhanhensis* n. sp.**

(Figs. 11–13, 21, 22D)

Zoobank: urn:lsid:zoobank.org:act:B5E8F34C-B815-4C5F-A221-230B67F003D4

Type material: Holotype, male (ISLA 50648), Brazil, Bahia, Serra do Ramalho, Carinhanha, Gruna da Água Clara Cave (-13,801182º -43,951733º), 11 October 2017, leg. R.L. Ferreira. Paratypes: 1 male (ISLA 50614) same data as holotype; 1 female (ISLA 50615), same data as holotype; 2 males 3 females (ISLA 50620), same data as holotype; 1 female (ISLA 50633), same data as holotype; 1 male (in slide) 2 females (ISLA50635), same data as holotype; 1 female (ISLA 50643), same data as holotype; 1 female (ISLA 50644), same data as holotype; 1 female (ISLA 50645), same data as holotype; 3 males, 13 female (ISLA 50653), same data as holotype; 1 male (ISLA 50655), same data as holotype; 1 female (ISLA 50656), same data as holotype; 2 females (ISLA 50674), same data as holotype; 1 male (ISLA 50649), same location as holotype, 10 October 2017; 1 female (ISLA 50646), same location as holotype, 12 October 2017; 1 female (ISLA 50650), same location as holotype, 12 October 2017; 1 male 1 female (ISLA 50673), same location as holotype, 12 October 2017; 1 female (ISLA 50630), same location as holotype, 16 October 2017; 1 female (ISLA 50647), same location as holotype, 16 October 2017; 2 females (ISLA50658), same location as holotype, 17 October 2017; 1 female (ISLA50632), Bahia, Serra do Ramalho, Carinhanha, Gruna dos Peixes II (-13.822815º -43.956776º), 14 October 2017; 1 female (ISLA 50651), same location; 1 female (ISLA 50659), same location, 10 October 2017; 1 female (ISLA 50661), same data; 1 female (ISLA 50641), Bahia, Serra do Ramalho, Carinhanha, Gruna dos Índios cave (-13,801308º -43,951374º), 14 October 2017.

Diagnosis. Antennula with eleven aesthetascs; male pleopod 1 exopod triangular, with round apex and sinuous lateral margin; male pleopod 2 exopod subtriangular, and pleopod 2 endopod apex twisted with pointed apex, directed outward.

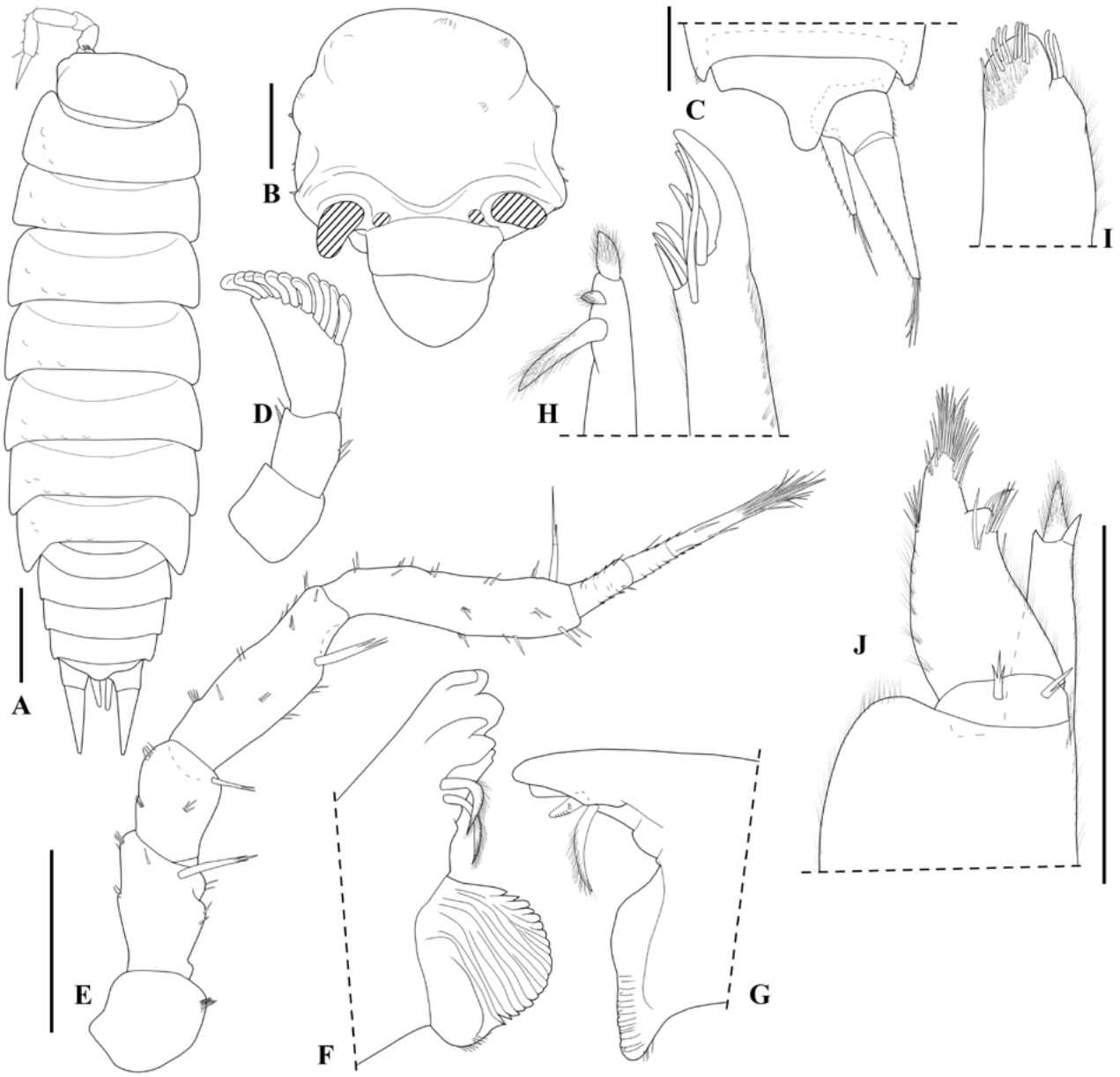

Figure 11. *Pectenoniscus carinhanhensis* n. sp. Male paratype: **A**, habitus, dorsal view; **B**, cephalon, frontal view; **C**, pleonite 5, pleotelson and uropod, dorsal view; **D**, antennula; **E**, antenna; **F**, left mandible; **G**, right mandible; **H**, maxillula; **I**, maxilla; **J**, maxilliped. Scale bars: **A**: 0,5 mm; **B**–**J**: 0.2 mm.

Description. Maximum length: male, 3.5 mm. Colorless, eyes absent (Figs. 11B, 13F). Dorsal granulations in three rows on pereonite 1, two on pereonites 2 to 7, smooth pleon (Fig. 11A, C). Cephalon with round antennal lobes; supra-antennal line bent in middle (Fig. 11A, B). Pereonite 1 with anterior margin not surpassing median portion of cephalon; pereonites 3–7 posterior margin progressively more concave; pleonites 3–5 epimera posterior point slightly developed; pleon narrower than pereon (Fig. 11A, C). Pleotelson with concave margin and round apex (Fig. 11C). Antennula with three articles, distal article with eleven aesthetascs (Fig. 11D). Antenna reaches distal margin of pereonite 2 when extended backward, fifth article of peduncle shorter than flagellum, with one seta longer than first flagellum article; flagellum with three articles (Fig. 11E). Left mandible with two penicils (Fig. 11F); right mandible with one penicil, *lacinia mobilis* leaf-shaped (Fig. 11G). Maxillula outer branch with 4+4 teeth, apically entire, and one plumose seta; inner branch with three penicils (Fig. 11H). Maxilla with bilobate apex, inner lobe wider

than outer lobe with several setae on distal margin (Fig. 11I). Maxilliped basis enlarged on distal portion; palp with two setae; endite triangular, apex with one triangular penicil and two lateral spines (Fig. 11J). Pereopod 1 antennal grooming brush composed of serrated scale setae on propodus and on sternal margin of carpus (Fig. 12B); dactylar seta bifid with thin setule. Uropod protopod triangular, as long as distal margin of pleotelson; exopod longer than endopod, inserted distally (Fig. 12A).

Male: Pereopods 6 and 7 (Fig. 12C, D) propodus with tufts of setae on tergal margin; with water conducting system; pereopod 7 ischium with straight sternal margin (Fig. 12D). Genital papilla (Fig. 12E) medial portion slightly enlarged with narrow apex. Pleopod 1 (Fig. 12E) protopod rectangular, two times wider than long; exopod triangular, with round apex and sinuous lateral margin; endopod longer than exopod. Pleopod 2 (Fig. 12F) protopod rectangular; exopod subtriangular, twice wider than long; endopod with distal article fourfold longer than proximal article, apex twisted with pointed apex, directed outward. Pleopod 3–5 exopods (Fig. 12F–H) trapezoidal, bearing setae on outer margin; exopod 5 with dorsal lobe.

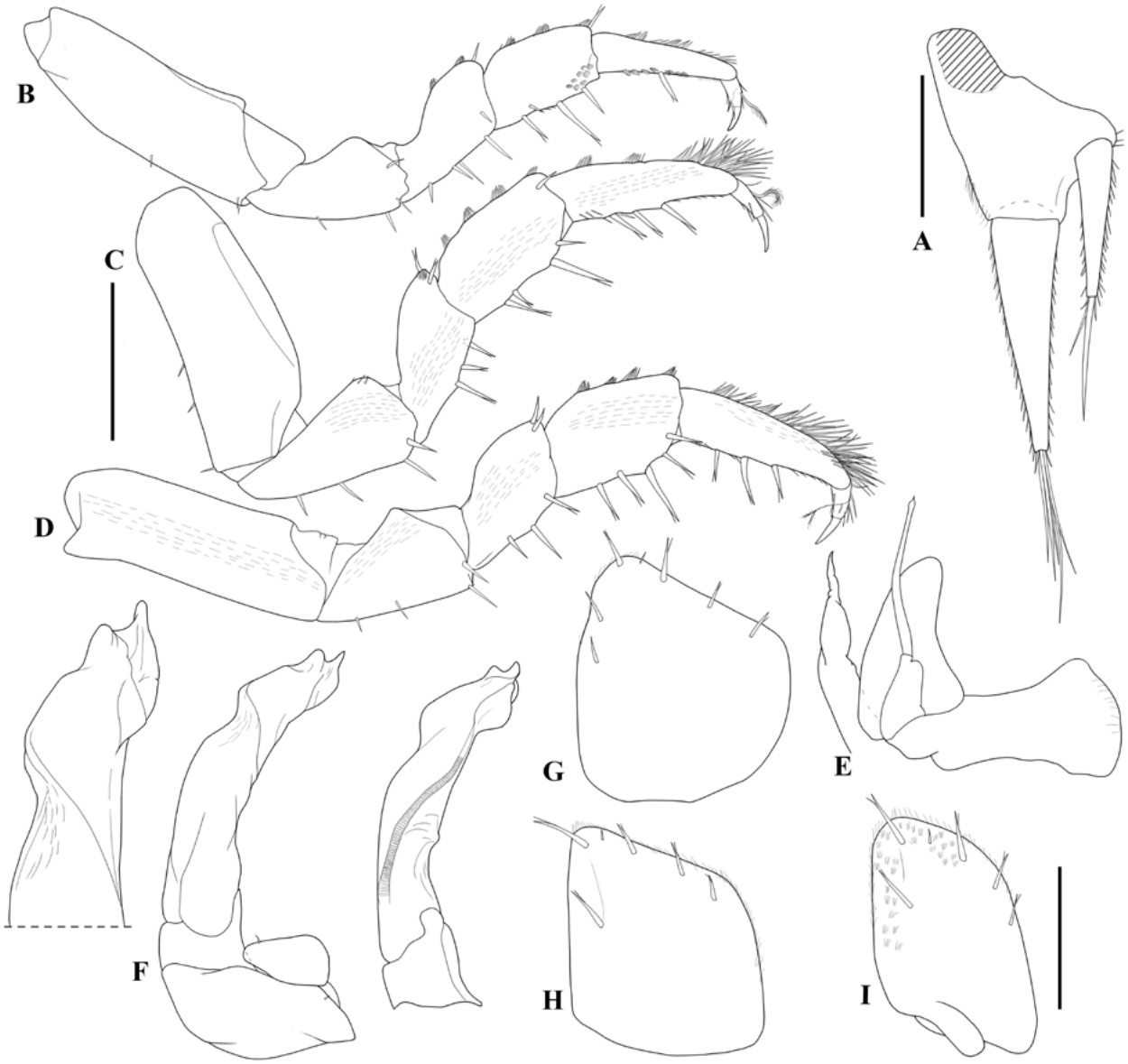

Figure 12. *Pectenoniscus carinhanhensis* n. sp. Male paratype: **A**, uropod; **B**, pereopod 1; **C**, pereopod 6; **D**, pereopod 7; **E**, genital papilla and pleopod 1; **F**, pleopod 2; **G**, pleopod 3 exopod; **H**, pleopod 4 exopod; **I**, pleopod 5 exopod. Scale bars: 0.2 mm.

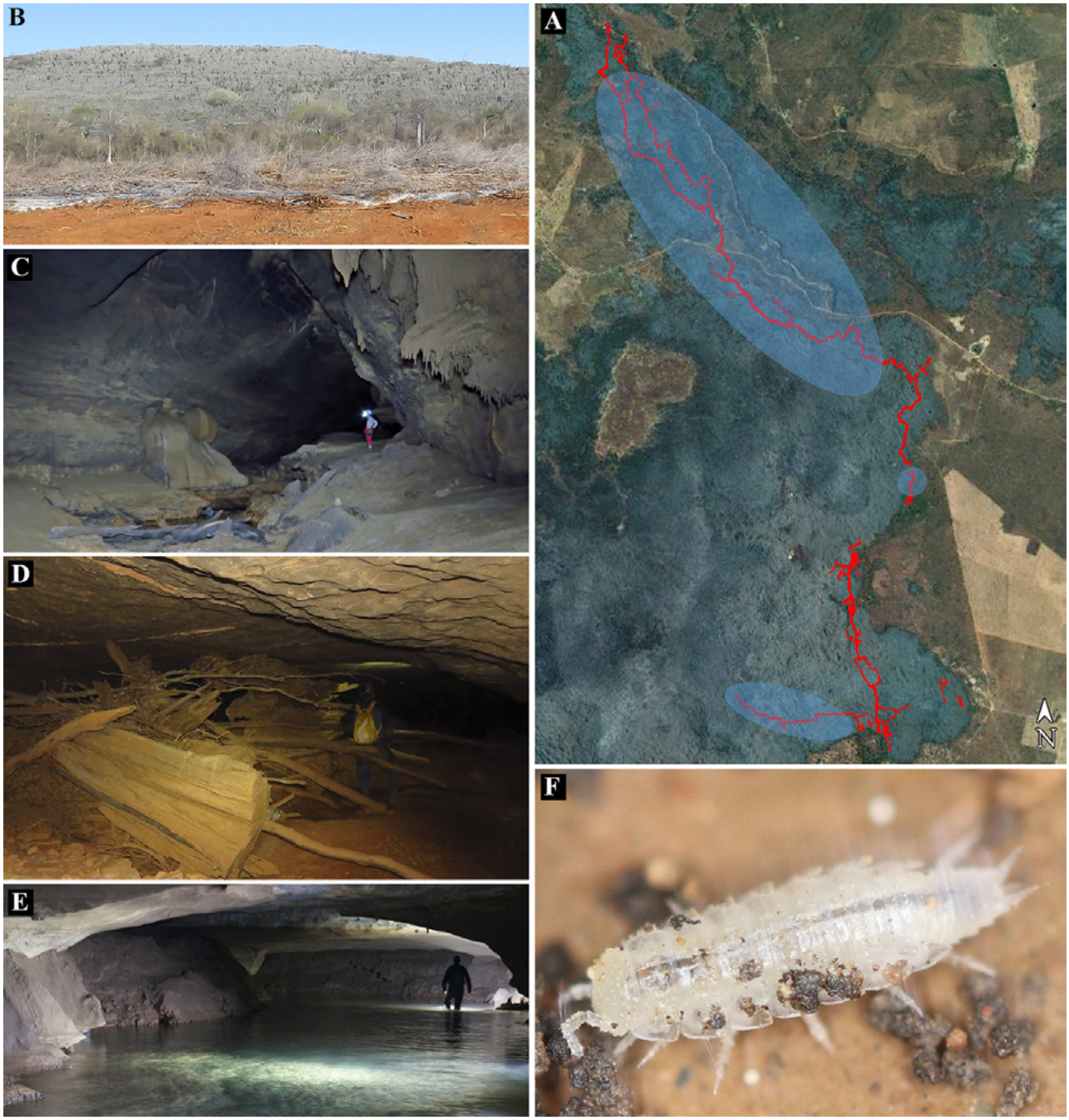

Figure 13. *Pectenoniscus carinhanhensis* n. sp. **A**, Águas Claras karst system (extension of caves in red, circles mark species occurrence; **B**, karst area of Serra do Ramalho; **C**, main conduit of Águas Claras cave; **D**, accumulated organic material in the conduit of Águas Claras cave; **E**, main conduit of Peixes II cave; **F**, specimen of *Pectenoniscus carinhanhensis* n. sp., approximately 3 mm.

Etymology. The specific epithet "*carinhanhensis*" refers to the municipality of Carinhanha (state of Bahia), where the new species was collected.

Remarks. *Pectenoniscus carinhanhensis* n. sp. differs from *P. angulatus* and *P. liliae* by the number of aesthetascs on antennula (11 *versus* 9 in *P. angulatus* and *P. liliae*), by the sternal margin of male pereopod 7 ischium (straight *versus* with a triangular projection in *P. angulatus* and convex margin in *P. liliae*), the shape of male pleopod 1 exopod (sinuous lateral margin *versus* straight in *P. angulatus* and *P. liliae*), the shape of male pleopod 2 exopod (subtriangular *versus* rectangular in *P. angulatus* and ovoid in *P. liliae*) and the orientation

of endopod (twisted *versus* straight in *P. angulatus* and *P. liliae*). *Pectenoniscus carinhanhensis* n. sp. is similar to *P. iuiuensis* n. sp. in the triangular shape of male pleopod 1 exopod, with round apex and sinuous lateral margin, however in *P. iuiuensis* n. sp. the exopod seems to be directed backward while in *P. carinhanhensis* n. sp. it is directed outward.

Habitat and ecological remarks. Specimens of *P. carinhanhensis* n. sp. were found in three caves of the Água Clara Cave System (ACCS) (Figs. 21, 22D). This system is formed by four limestone caves interconnected by an intermittent drainage (Gruna da Água Clara, Gruna dos Índios, Lapa dos Peixes I, and Lapa dos Peixes II – Fig. 13A). Two of the caves that compose the system are the tenth and the fourteenth biggest caves in Brazil, respectively (Água Clara Cave – 13,880 meters and Lapa dos Peixes cave – 9,320 meters long), while the other two are smaller (Gruna dos Índios cave – 570 meters and Lapa dos Peixes II – 2,100 meters). Together these four caves account for 25.85 km of subterranean passages. In general, the caves present wide vadose conduits (Fig. 13C, E) through which a huge amount of water flows during the rainy periods, noticeable by the massive plant debris (such as tree trunks) observed at several points within the caves (Fig. 13D). Although the water flows along the caves only in the rainy periods, flooded chambers occur in some areas even in the dry periods, as in the Lapa dos Peixes II cave (Fig. 13E). Individuals of *P. carinhanhensis* n. sp. were observed in several areas along the caves, always associated with moist substrates (Fig. 13F). Most specimens (around 90% of the observed specimens in the ACCS) were found in Água Clara cave (Fig. 13C), which is the first (upstream) and biggest cave of the ACCS. The large number of specimens observed in this cave (dozens of individuals) can be related to its high humidity throughout the whole year, due to its dimensions. Few specimens (less than 10) were observed in Lapa do Índio cave, where they were restricted to a few moistened areas (a considerable extension of the cave was dry when the sampling was carried out). Finally, specimens were also collected in Lapa dos Peixes II cave, the last (downstream) cave of the ACCS. Although this species was not found in Lapa dos Peixes cave I, the possibility of its occurrence in this cave is not excluded, since only part of this cave was inventoried. In this sense it is plausible to assume that this species occurs in the whole ACCS. Specimens of *P. carinhanhensis* n. sp. were observed in very distinct conditions regarding the presence of visible organic matter. In some areas they were encountered close to vegetable debris, while in the deeper portions of the caves (especially in Água Clara cave) organisms were found in areas completely devoid of visible organic resources. The ACCS also shelters six other troglobitic species: the isopod *Xangoniscus aganju* Campos-Filho, Araujo and Taiti, 2014, the harvestmen *Giupponia chagasi* Pérez and Kury, 2002 (Kury and González, 2002), the whip spider *Charinus troglobius* Baptista and Giupponi, 2002, the earwig *Mesodiplatys falcifer* Kamimura and Ferreira, 2018, the snail *Spiripockia punctata* Simone, 2012 and the fish *Trichomycterus rubiolli* Bichuette and Rizatto, 2012. The native habitat surrounding the caves consists of the Caatinga formation, which is severely altered, especially due to the removal of the original vegetation for charcoal production, as well as for the establishment of pastures and monocultures (Fig. 13B). The caves seem to be only visited by speleologists, so that the impacts of trampling over the cave fauna is negligible.

***Pectenoniscus santanensis* n. sp.**

(Figs. 14–16, 21, 22E)

Zoobank: urn:lsid:zoobank.org:act:0DB726B3-9C0D-4912-846A-8F2E9AC553F8

Type material. Holotype: male (ISLA 77532) (slide), Bahia, Santana, Gruta do Padre cave (-13.216325º -44.065194º), 18 July 2019, leg. R.L. Ferreira. Paratype. 1 female (ISLA 77533), same locality as holotype, 18 July 2019, leg. R.L. Ferreira.

Diagnosis. Antennula with six aesthetascs; male pleopod 1 exopod triangular, with lateral margin straight and round apex; male pleopod 2 exopod subtriangular; and male pleopod 2 endopod twisted and apex forked.

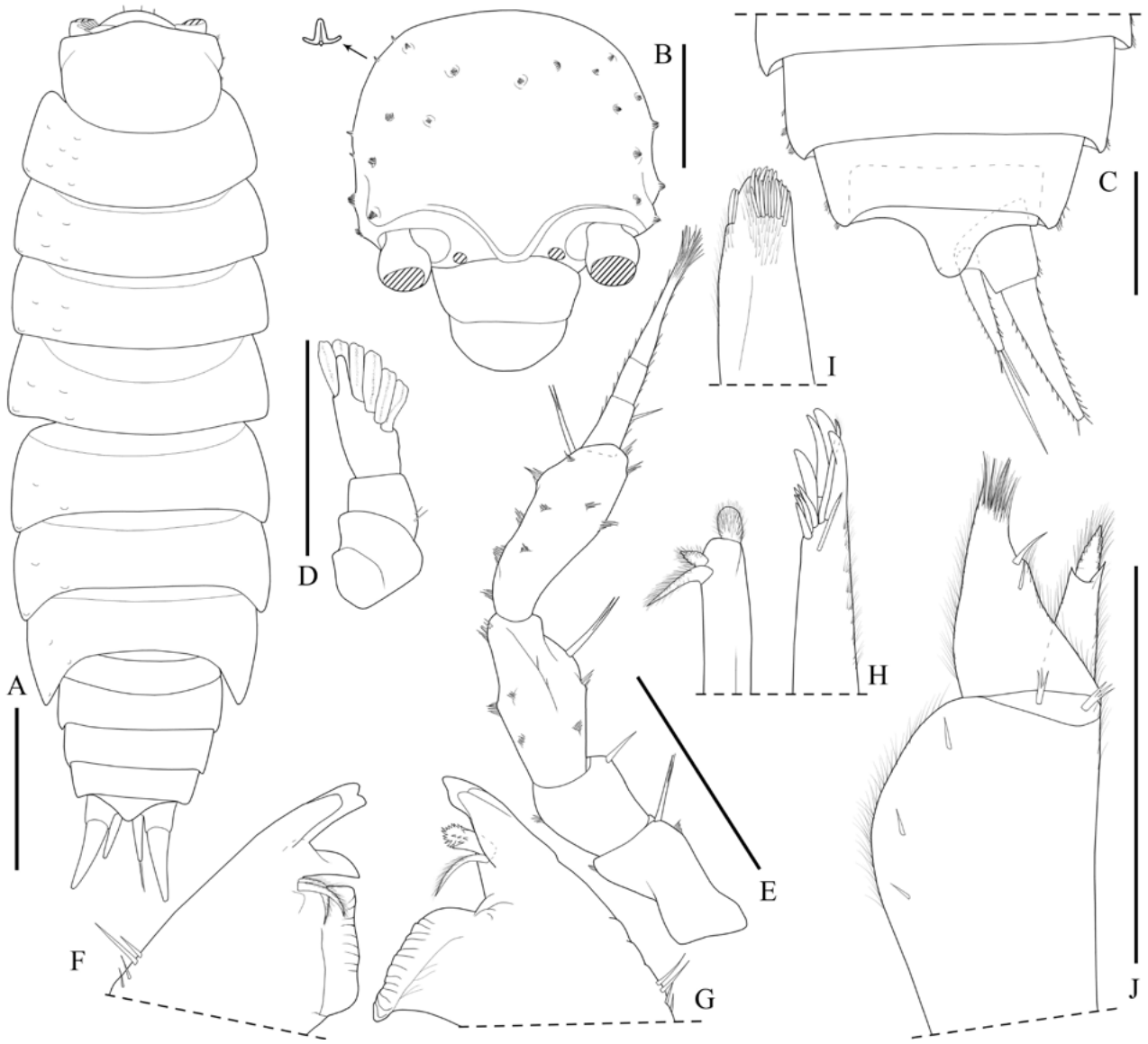

Figure 14. *Pectenoniscus santanensis* n. sp. Female paratype: **A**, habitus, dorsal view; **B**, cephalon, frontal view; **C**, pleonites 3–5, pleotelson and uropod, dorsal view; **D**, antennula; **E**, antenna; **F**, left mandible; **G**, right mandible; **H**, maxillula; **I**, maxilla; **J**, maxilliped. Scale bars: **A**: 0,5 mm; **D**: 0,1 mm; **B, C, E–J**: 0.2 mm.

Description. Maximum length: male, 2 mm. Colorless, eyes absent (Figs. 14A, 16D). Dorsal scale-setae tricorn-shaped (Fig. 14B). Dorsal granulations in two rows on pereonites 1 to 7, smooth pleon (Fig. 14A, C). Cephalon with round antennal lobes; supra-antennal line bent in middle (Fig. 14B). Pereonite 1 with margin projected forward, not surpassing median portion of cephalon; pereonites 4–7 posterior margin progressively more concave; pleonites 3–5 epimera posterior points slightly developed; pleon narrower than pereon (Fig. 14A). Pleotelson with concave margin and round apex (Fig. 14C). Antennula with three articles, distal article with six aesthetascs (Fig. 14D). Antenna surpasses pereonite 1 when extended backward, fifth article of peduncle shorter than flagellum, with one seta as long as first flagellum article; flagellum with three articles (Fig. 14E). Left mandible with two penicils (Fig. 14F); right mandible with one penicil, *lacinia mobilis* leaf-shaped (Fig. 14G). Maxillula outer branch with 4+5 teeth, apically entire, and two plumose setae; inner branch with three penicils (Fig. 14H). Maxilla with bilobate apex, inner lobe wider than outer lobe with several setae on distal margin (Fig. 14I). Maxilliped basis enlarged on distal

portion; palp with two setae; endite triangular, apex with one penicil and two spines (Fig. 14J). Pereopod 1 antennal grooming brush composed of serrated scale setae on propodus and on sternal margin of carpus (Fig. 15A); dactylar seta bifid with thin setule. Uropod protopod rectangular, longer than distal margin of pleotelson; exopod longer than endopod, inserted distally (Fig. 14C).

Male: Pereopods 6 and 7 (Fig. 15B, C) propodus with tufts of setae on tergal margin, with water conducting system; pereopod 7 ischium with straight sternal margin (Fig. 15C). Genital papilla (Fig. 15D) with medial portion slightly enlarged with narrow apex. Pleopod 1 (Fig. 15D) protopod rectangular, three times wider than long; exopod triangular, with lateral margin straight and round apex; endopod more than twice longer than exopod. Pleopod 2 (Fig. 15E) protopod rectangular; exopod subtriangular, almost twice wider than long; endopod with distal article three times longer than proximal article, twisted, apex forked (two distal projections, one directed backward and one outward). Pleopod 3–5 exopods (Fig. 15F–H) subquadrangular, bearing four-five setae on outer margin.

Etymology. The specific epithet "*santanensis*" refers to municipality of Santana, where the new species was collected.

Remarks. Pectenoniscus santanensis n. sp. differs from *P. angulatus* and *P. liliae* by the dorsal granulation pattern (two rows in all the pereonites *versus* three rows in the first pereonite and two in the others on *P. angulatus* and *P. liliae*), the number of aesthetascs on antennula (6 *versus* 8 in *P. angulatus* and 9 in *P. liliae*), the sternal margin of male pereopod 7 ischium (straight *versus* with triangular projection in *P. angulatus* and convex in *P. liliae*), the shape of male pleopod 2 exopod (sub-triangular *versus* rectangular in *P. angulatus* and ovoid in *P. liliae*) and the orientation of male pleopod 2 endopod (twisted *versus* straight in *P. angulatus* and *P. liliae*). *Pectenoniscus santanensis* n. sp. is similar to *P. carinhanhensis* n. sp. in the shape of male pleopod 2 exopod subtriangular and by the straight sternal margin of male pereopod 7 ischium; however it differs by the number of aesthetascs on antennula (6 *versus* 11 in *P. carinhanhensis* n. sp.) and the shape of male pleopod 1 exopod (straight lateral margin *versus* sinuous in *P. carinhanhensis* n. sp.).

Habitat and ecological remarks. Gruta do Padre represents one of the largest known caves in Brazil (16,400 meters of horizontal projection – Fig. 16A), currently considered the fifth longest in total extension in the country (Rubbioli *et al.*, 2019) and is part of one of the most extensive subterranean hydrological systems in Brazil. It presents three distinct levels with a river flowing in the lowest one (Fig. 16C). The upper level is accessed through the cave main entrance (Fig. 16B), and is connected to a set of ample galleries, most of which were enlarged by collapsing processes. The specimens were found on the floor, walking on a moist mud layer, in a voluminous chamber located in a deep portion of the upper level, around 500 meters from the main cave entrance (Fig. 16D). Although far from the river, the substrates were moist due to the high humidity in the chamber provided by dripping speleothems. Considering the huge dimensions of the cave, a thorough search was only performed in few areas, therefore the low number of registered specimens (less than 10 – some of them were not collected) does not necessarily indicate that the species present low population density. Gruta do Padre cave also presents other described troglobitic species, such as the beetle *Coarazuphium tessai* (Godoy and Vanin, 1990), the amphipod *Spelaeogammarus santanensis* Koenemann and Holsinger, 2000 and the millipede *Phaneromerium cavernicolum* Golovatch and Wytwer, 2004. Currently, the external environment surrounding the cave is altered, especially by the removal of the native vegetation for pastures (Figs. 21, 22E). On the other hand, considering the huge extension of the cave and the fact that only a few speleologists visit it each year (especially due to the difficult accesses inside the cave), the inner portion of the cave is well preserved.

***Pectenoniscus morrensis* n. sp.**

(Figs. 17–20, 21, 22F)

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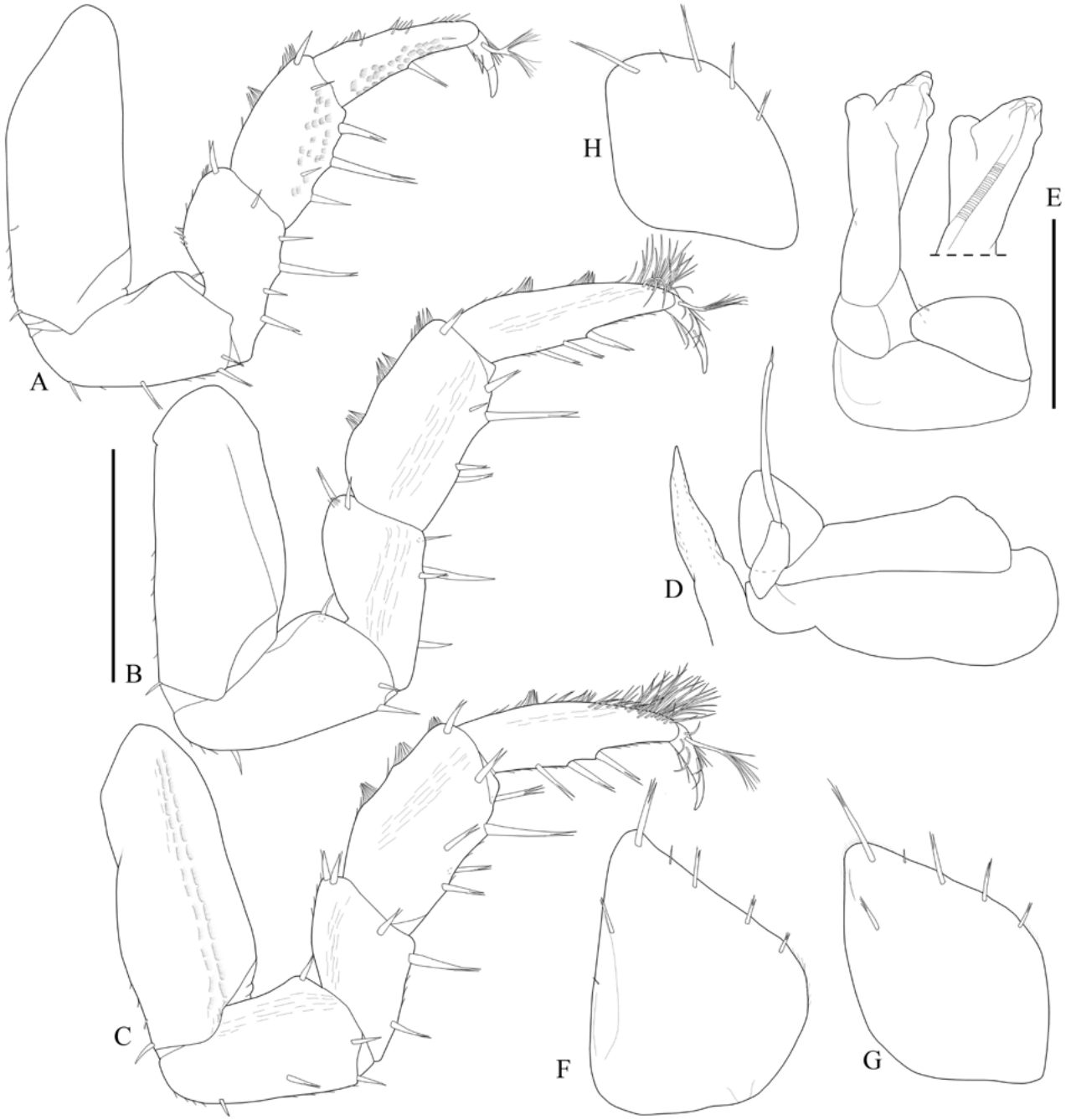

Figure 15. *Pectenoniscus santanensis* n. sp. Male holotype: **A**, pereopod 1; **B**, pereopod 6; **C**, pereopod 7; **D**, genital papilla and pleopod 1; **E**, pleopod 2; **F**, pleopod 3 exopod; **G**, pleopod 4 exopod; **H**, pleopod 5 exopod. Scale bars: 0.2 mm.

Type material. Holotype: male (ISLA 77534), Brazil, Bahia, Morro do Chapéu, Gruta dos Brejões cave (-11.007225° -41.435169°), 23 January 2012, leg. R.L. Ferreira. Paratypes: 7 males, 7 females (ISLA 77535), same data as holotype.

Diagnosis. Male pleopod 1 exopod triangular with lateral margin straight, round apex; endopod more than twice longer than exopod; male pleopod 2 exopod subtriangular, and endopod apex twisted with lateral projection directed outward.

Figure 16. *Pectenoniscus santanensis* n. sp. **A**, Gruta do Padre cave map, the dotted line represents the upper level, with collecting site; **B**, entrance of Gruta do Padre cave, inside the cave; **C**, main conduit of Gruta do Padre cave; **D**, specimen of *Pectenoniscus santanensis* n. sp., approximately 2 mm.

Description. Maximum length: male, 2 mm. Colorless, eyes absent (Figs. 17A, 19A, 20F). Dorsal scale-setae tricorn-shaped (Fig. 19A, B). Dorsal granulations in two rows on pereonites 1 to 7, smooth pleon (Fig. 19B, C). Cephalon with round antennal lobes; supra-antennal line bent in middle (Fig. 19A). Pereonite 1 with margin projected forward, not surpassing median portion of cephalon; pereonites 4–7 posterior margin progressively more concave; pleonites 3–5 epimera posterior points slightly developed; pleon narrower than pereon (Figs. 17A, 19C). Pleotelson with concave margin and round apex (Fig. 17B). Antennula with three articles, distal article with six aesthetascs (Fig. 17C). Antenna surpasses pereonite 2 when extended backwards, fifth article of peduncle shorter than flagellum, with one seta longer than the second flagellum article; flagellum with three articles (Fig. 17D). Left mandible with two penicils (Fig. 17E); right mandible with one penicil, *lacinia mobilis* leaf-shaped (Fig. 17F). Maxillula outer branch with 4+5 teeth, apically entire, and one plumose seta; inner branch with three penicils (Fig. 17G).

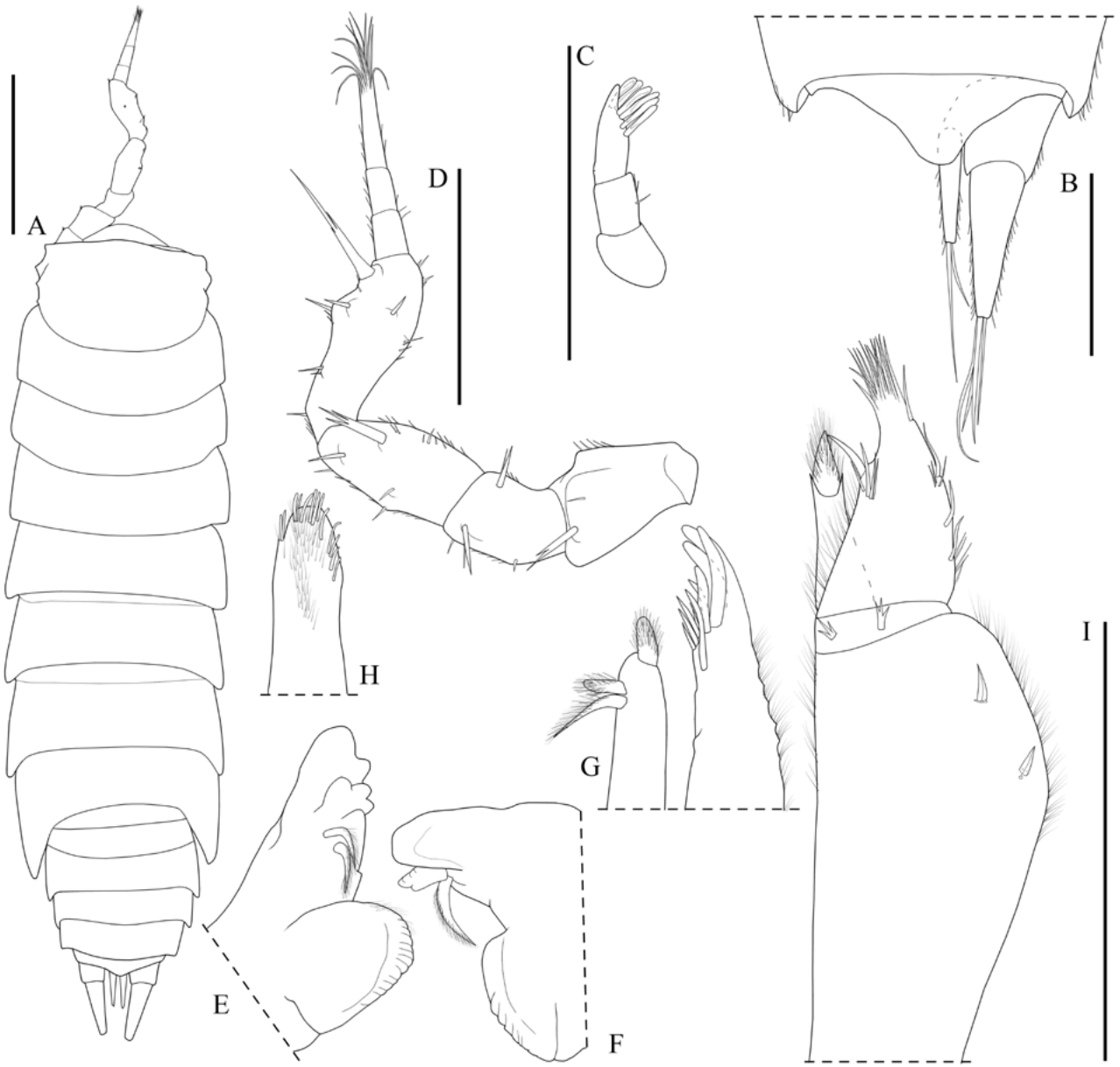

Figure 17. *Pectenoniscus morrensis* n. sp. Male paratype: **A**, habitus, dorsal view; **B**, cephalon, frontal view; **C**, pleonite 5, pleotelson and uropod, dorsal view; **D**, antennula; **E**, antenna; **F**, left mandible; **G**, right mandible; **H**, maxillula; **I**, maxilla; **J**, maxilliped. Scale bars: **A**: 0,5 mm; **B**–**J**: 0.2 mm.

Maxilla with bilobate apex, inner lobe wider than outer lobe with several setae on distal margin (Fig. 17H). Maxilliped basis enlarged on distal portion; palp with two setae; endite triangular, apex with one penicil and two spines (Fig. 17I). Pereopod 1 antennal grooming brush composed of serrated scale setae on propodus and on sternal margin of carpus (Fig. 18A); dactylar seta bifid with thin setule. Uropod protopod rectangular, longer than distal margin of pleotelson; exopod longer than endopod, inserted distally (Fig. 17B).

Male: Pereopods 6 and 7 propodus with tufts of setae on tergal margin; water conducting system; pereopod 7 ischium with convex sternal margin (Fig. 18B, C). Genital papilla (Fig. 18D) with medial portion slightly enlarged with narrow apex. Pleopod

1 (Fig. 18D) protopod rectangular, two times wider than long; exopod triangular, lateral margin straight, round apex; endopod more than twice longer than exopod. Pleopod 2 (Fig. 18E) protopod rectangular; exopod subtriangular, almost twice wider than long; endopod with distal article three times longer than proximal article, apex twisted with lateral projection directed outward. Pleopod 3–5 exopods (Fig. 18F–H) subquadrangular, bearing five, four and three setae on outer margin, respectively.

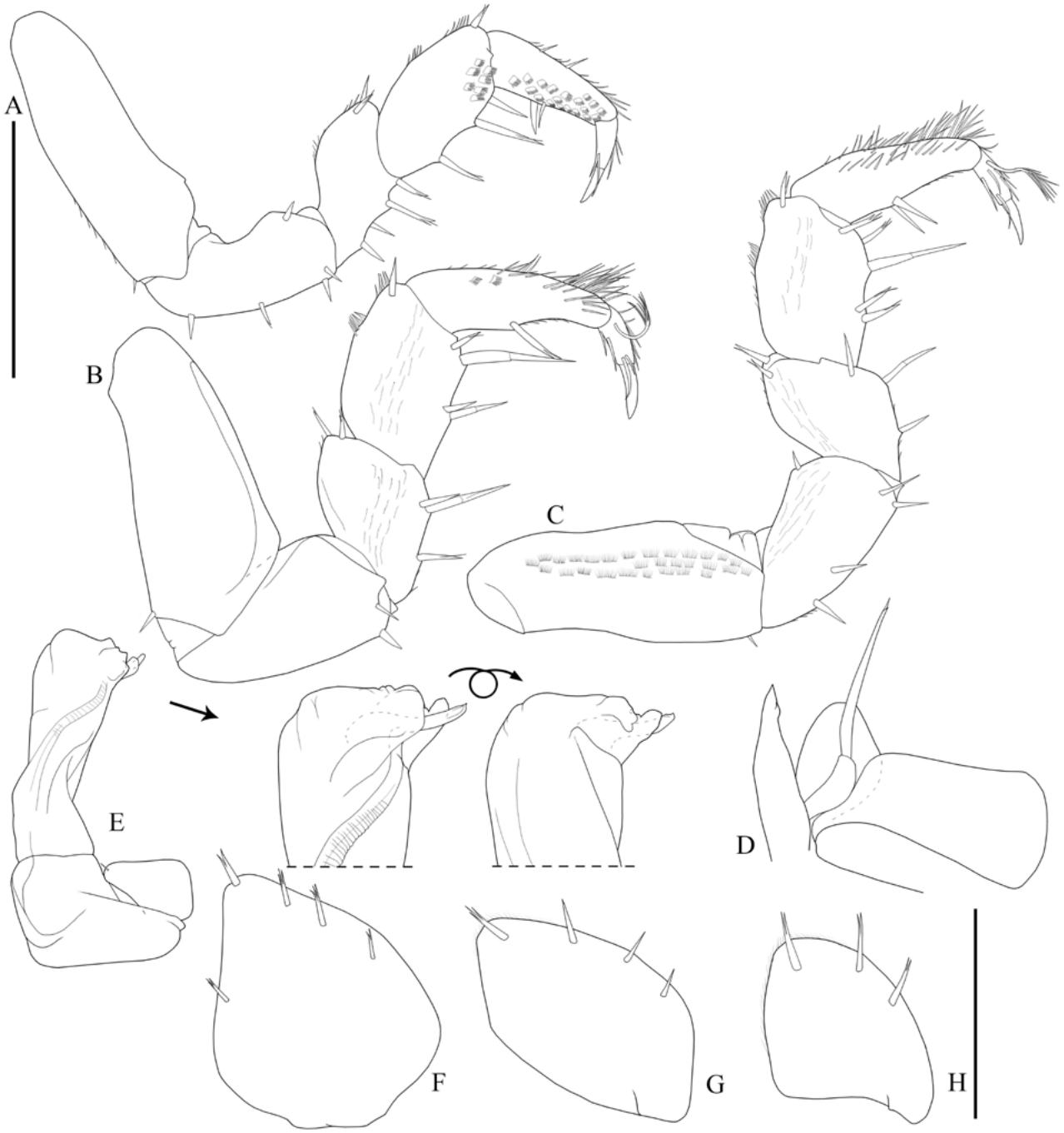

Figure 18. *Pectenoniscus morrensis* n. sp. Male paratype: **A**, pereopod 1; **B**, pereopod 6; **C**, pereopod 7; **D**, genital papilla and pleopod 1; **E**, pleopod 2; **F**, pleopod 3 exopod; **G**, pleopod 4 exopod; **H**, pleopod 5 exopod. Scale bars: 0.2 mm.

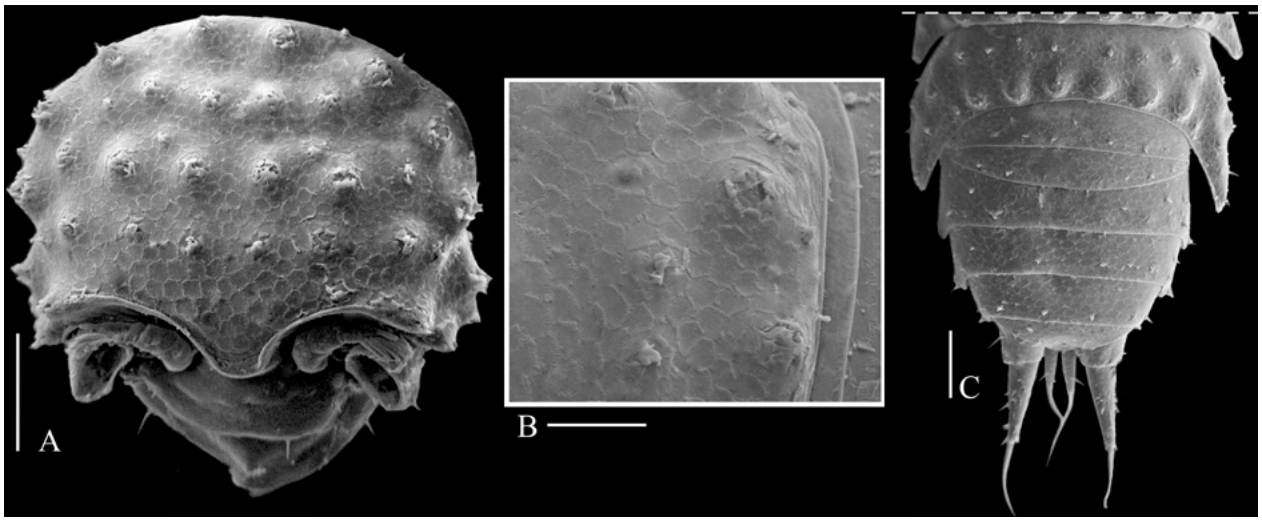

Figure 19. *Pectenoniscus morrensis* n. sp. Female paratype: **A**, cephalon, frontal view; **B**, epimeron 1, dorsal view; **C**, pleonite 7, pleon, pleotelson and uropods, dorsal view. Scale bar: **A, C**: 100μm; **B**: 40μm.

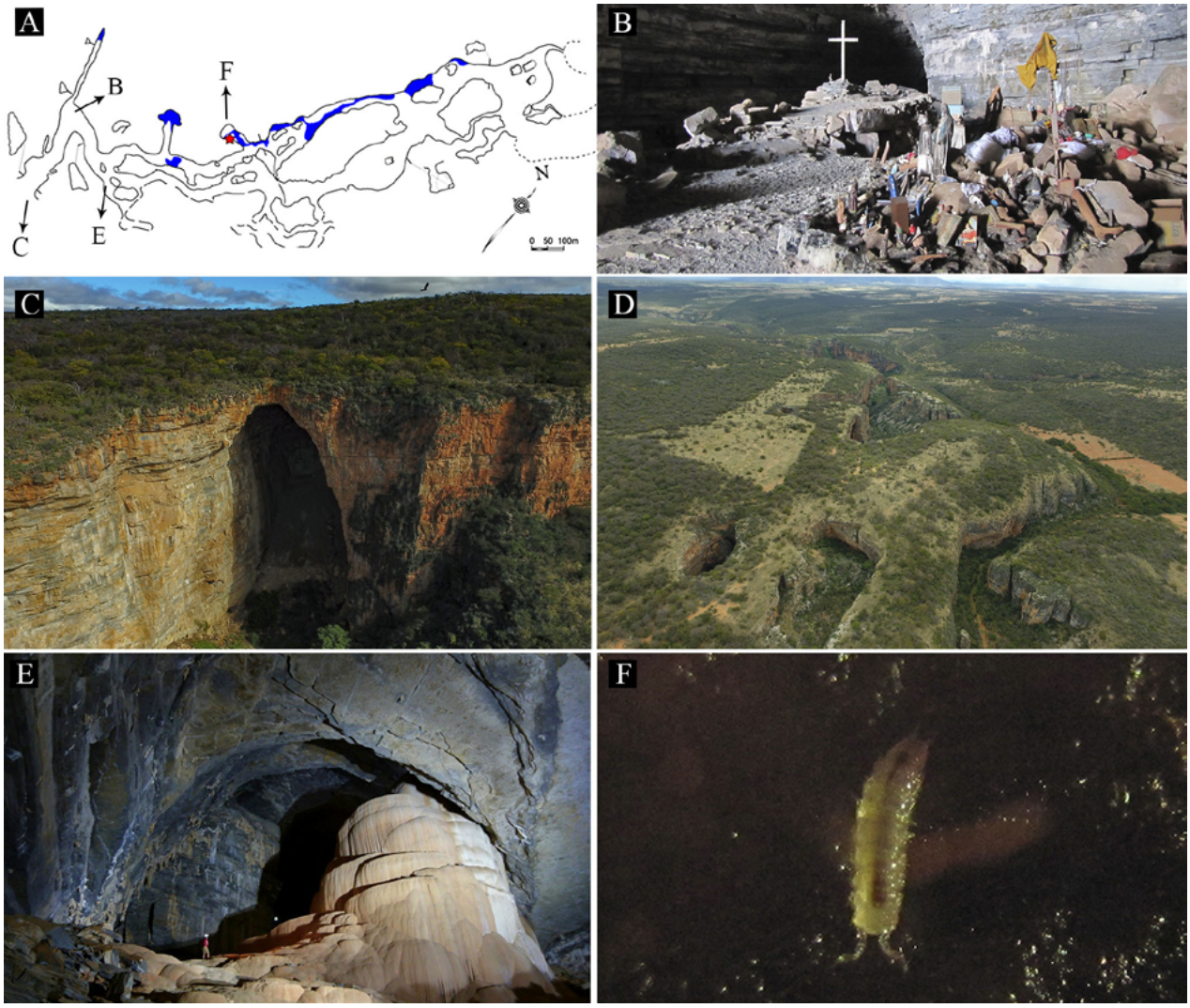

Figure 20. *Pectenoniscus morrensis* n. sp. **A**, Gruta dos Brejões cave map, with collecting site; **B**, religious site in Gruta dos Brejões cave; **C**, entrance of Gruta dos Brejões cave, outside view; **D**, aerial photograph of the Permanent Preservation Area of Gruta dos Brejões; **E**, travertine dams, locally known as "wedding cake" or the "altar", one of the main speleothems of the cave; **F**, specimen of *Pectenoniscus morrensis* n. sp.

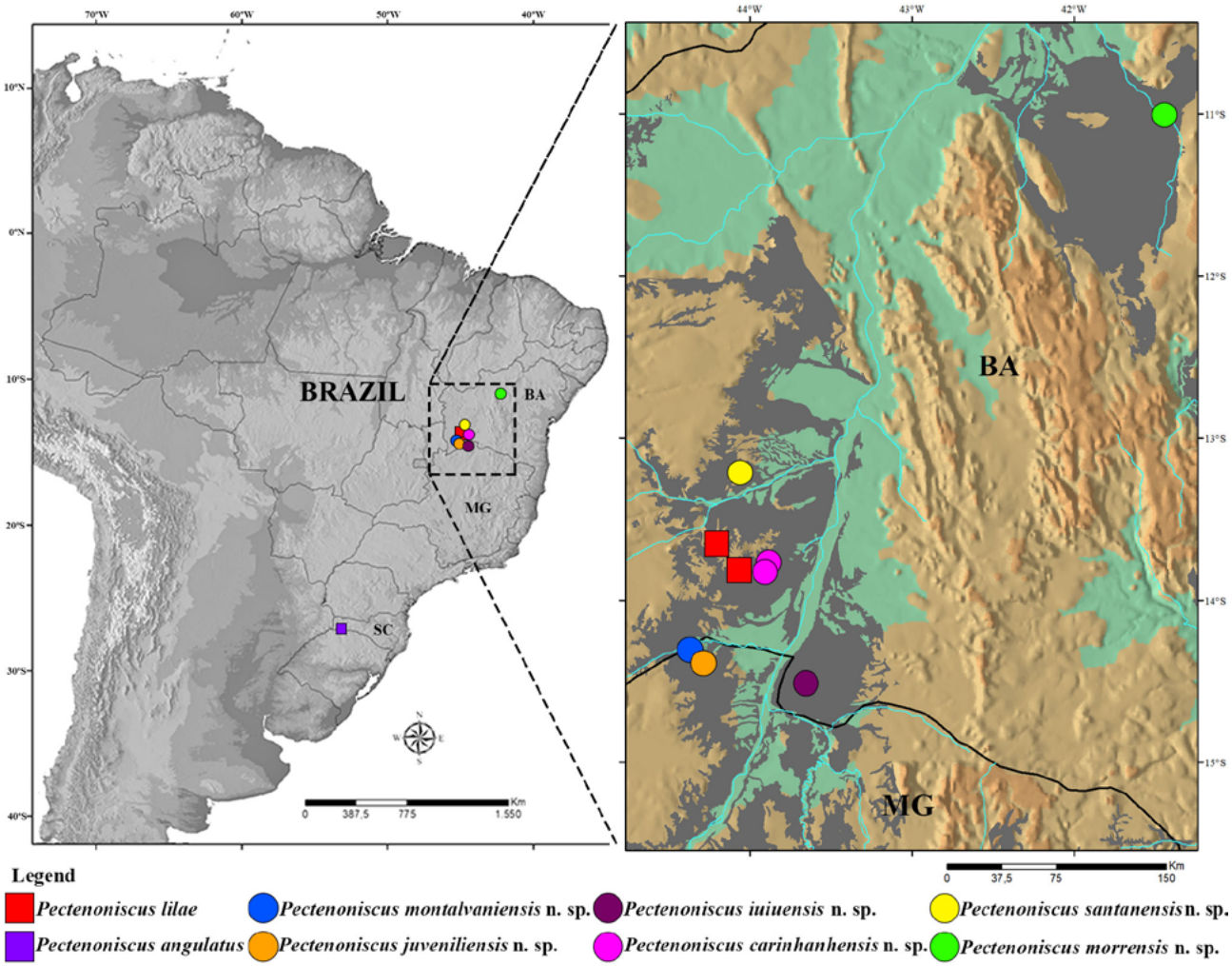

Figure 21. Map of South America highlighting Brazil and the states of Bahia (BA), Minas Gerais (MG), and Santa Catarina (SC), where the species of *Pectenoniscus* are recorded. Brown and green colors indicate the elevation of the terrain, with brown for higher levels, green for lower levels; gray indicates karstic areas.

Etymology. The specific epithet "*morrensis*" refers to the municipality of Morro do Chapéu, where the new species was collected.

Remarks. *Pectenoniscus morrensis* n. sp. differs from *P. angulatus* and *P. liliae* by the dorsal granulation pattern (two rows in all the pereonites *versus* three rows in the first pereonite and two in *P. angulatus* and *P. liliae*), the number of aesthetascs on antennula (6 *versus* 8 in *P. angulatus* and 9 in *P. liliae*), the shape of male pleopod 2 exopod (subtriangular *versus* rectangular in *P. angulatus* and ovoid in *P. liliae*) and the orientation of endopod (twisted *versus* straight in *P. angulatus* and *P. liliae*). *Pectenoniscus morrensis* n. sp. is similar to *P. santanensis* n. sp. in the number of aesthetascs on antennula, by the shape of male pleopod 1 exopod triangular with lateral margin straight and round apex; and by the shape of male pleopod 2 exopod subtriangular, however, it differs by the shape of male pleopod 2 endopod.

Habitat and ecological remarks. Specimens of *P. morrensis* n. sp. were found in Gruta dos Brejões cave, located in the municipality of Morro do Chapéu (state of Bahia) (Fig. 21). The cave presents an impressive entrance of 106 meters high (Fig. 20C) followed by a chamber with similar dimensions. The cave extends 6,570 meters, but it was longer in the past, trespassing a massive limestone outcrop (Figs. 20C, D, 21F). During the karst evolution in the area most of its original conduit collapsed, creating a canyon (Fig. 20D). In fact, the cave presents two conduits (Gruta I e II) laterally connected in some areas. The upper level is predominantly dry and presents huge skylights and impressive speleothems (Fig. 20E). On the other hand, the lower level is moist due to the presence of the Jacaré river, which arises among collapsed blocks (around 750 meters from the main entrance) and covers a considerable extension of the lower level. There are ponds connected to the river in some areas of the lower level in which a thin layer of calcite is deposited on the water surface. When the water level drops, such pieces of calcite are deposited on the muddy sediment of the riverbanks. Individuals of *P. morrensis* n. sp. were found under those calcite fragments walking on the substrate (Fig. 20F). The organic resources observed in this area were a few small fragments of vegetal debris, transported to the cave by the river. This river shelters the unique troglobitic Porifera from Brazil (the sponge *Racekiela cavernicola* Volkmer-Ribeiro, Bichuette and De Sousa Machado, 2010), which is extremely abundant on the riverbed, presenting hundreds of individuals. Another troglobitic species inhabiting the cave is the spider *Ariadna aurea* Giroti and Brescovit, 2018. The external landscape surrounding the cave is altered. Although the upper part of the limestone outcrop is well preserved in some areas (due to the difficulties of access), the Jacaré river valley is severely altered especially because it constitutes the only water source in the region. There are many crops grown in the valley (Fig. 22F).

Identification key

1 Dorsal granulation pattern composed of two rows in all the pereonites 2

1' Dorsal granulation pattern composed of three rows in the first pereonite and two in the second to seventh 4

2 Six aesthetascs in the distal article of antennule ..3

2' Nine aesthetascs in the distal article of antennule, male pleopod 1 exopod with acute apex, male pleopod 2 endopod apex round with two subapical lobes on inner margin (Fig. 5C) ..... *P. juveniliensis* n. sp.

3 Male pleopod 2 endopod twisted with forked apex (Fig. 15E) ..... *P. santanensis* n. sp.

3' Male pleopod 2 endopod apex twisted with lateral projections directed outwards (Fig. 18E)..... *P. morrensis* n. sp.

4 Antenna flagellum with less than five articles ... 5

4' Antenna flagellum with five articles, male pereopod 7 ischium with a triangular projection on sternal margin, male pleopod 2 endopod straight, directed frontward ..... *P. angulatus*

5 Male pleopod 1 exopod with rounded apex and sinuous lateral margins (Figs. 9D, 12E)..... 6

5' Male pleopod 1 exopod with rounded apex and straight lateral margins 7

6 Distal article of antennule with 10 aesthetascs, male pleopod 2 exopod subrectangular, endopod wrench-like shape and round apex with bifid distal projection (Fig. 9E) ..... *P. iuiuensis* n. sp.

6' Distal article of antennule with 11 aesthetascs, male pleopod 2 exopod subtriangular, endopod apex twisted with pointed apex directed outward (Fig. 12F) ..... *P. carinhanhensis* n. sp.

7 Male pleopod 2 exopod ovoid, endopod apical chela-shaped with 2 triangular lobes..... *P. liliae*

7' Male pleopod 2 exopod trapezoid, endopod distal lobe directed inward with subapical denticles projected outward (Fig. 2F) ..... *P. montalvaniensis* n. sp.

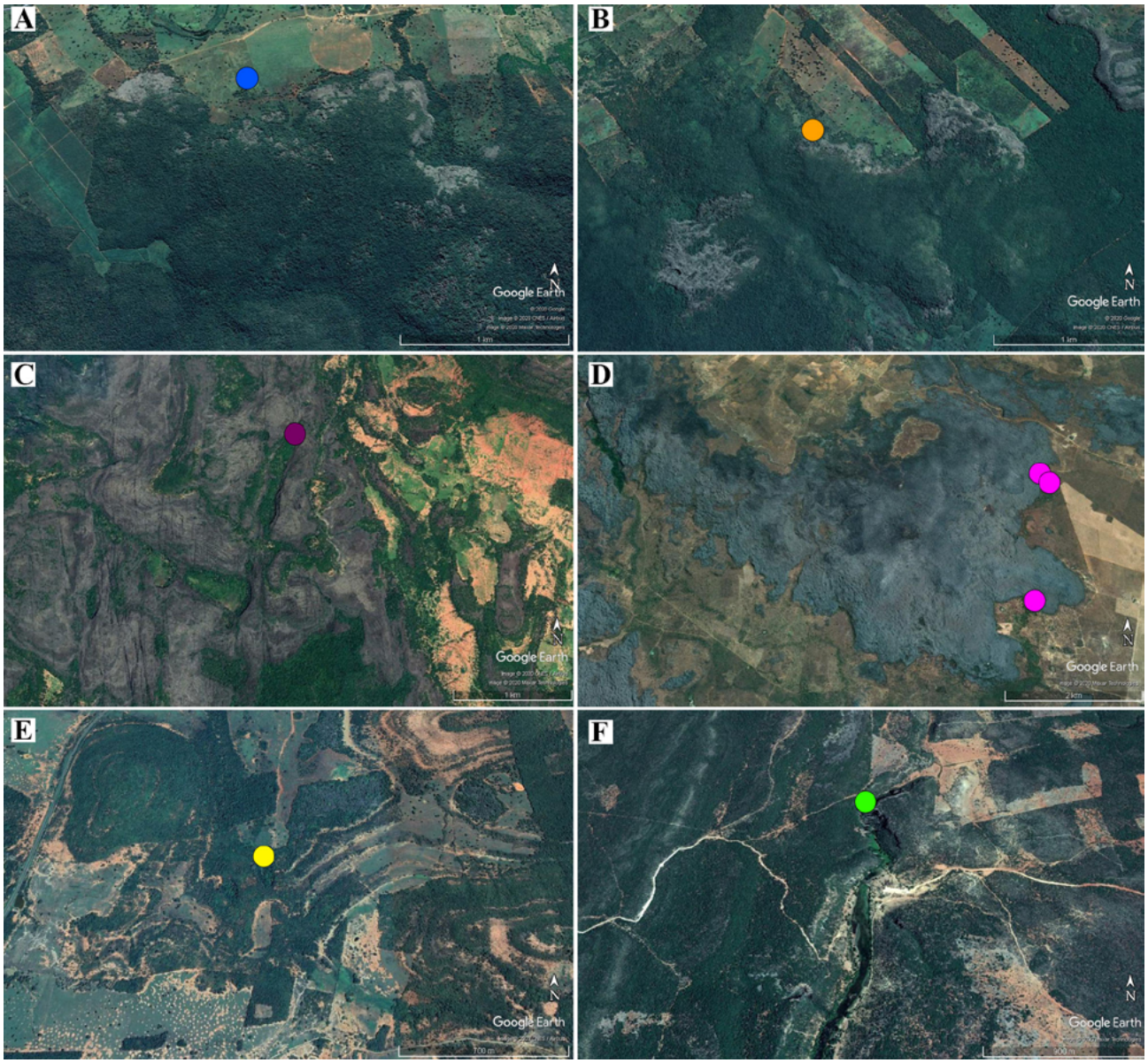

Figure 22. Satellite images of localities: **A**, Abrigo da Ema (Montalvânia municipality); **B**, Gruta do Tabuleirinho (Juvenilia municipality); **C**, Baixa da Fortuna cave (Iuiu municipality); **D**, Gruna da Água Clara Cave, Gruna dos Índios cave and Gruna dos Peixes II, from top to bottom (Carinhanha municipality); **E**, Gruta do Padre cave (Santana municipality); **F**, Gruta dos Brejões (Morro do Chapéu municipality).

Discussion

Although *Pectenoniscus* was described sixty years ago (Andersson, 1960), the second species of this genus was only recently described (Campos-Filho *et al.*, 2019). In this sense, the knowledge of this genus was restricted to the description of two species until the present; thus limiting the possibilities of interpretations on adaptive characteristics of the group to the subterranean habit.

Regarding epigean representatives of Styloniscidae worldwide, *Madoniscus termitis* Paulian de Félice, 1950 and *P. angulatus* are the uniquely depigmented and anophthalmic species. *Madoniscus termitis* is a termitophilous oniscidean found in the Tampolo forest in Madagascar. This species taxonomic placement is questionable, since it was allocated first into the family Trichoniscidae (Paulian de Félice, 1950) and later mentioned as part of Styloniscidae by Taiti (2018)

when describing another termitophilous species (*Ctenorillo meyeri*, Armadillidae).

In *Clavigeroniscus* Arcangeli, 1930, despite the three ommatidia being described as a diagnostic character of the genus, the species *Clavigeroniscus mussaui* Vandel, 1973 may present some variation in such a character, as well as in the body pigmentation. Vandel (1973) mentions that the most common color is dark brown, although some specimens may be light brown, purple or yellowish. In this sense, this author indicates that this species presents a tendency to anophthalmia and depigmentation, even occurring in leaf litter. Considering other genera of Styloniscidae found in epigean environments (*Styloniscus* Dana, 1853, *Cordioniscus* Graeve, 1914, *Indoniscus* Vandel, 1952), the species in general are pigmented and present three ommatidia arranged in a triangle (*e.g.*, Vandel, 1973; Gregory and Lugg, 2018). On the other hand, *Spelunconiscus, Xangoniscus, Trogloniscus* Taiti and Xue, 2012, *Thailandoniscus* Dalens, 1989 and *Bamaoniscus* Taiti and Montesanto, 2020 are composed of strictly subterranean species and all of them are eyeless and depigmented (Taiti and Xue, 2012; Campos-Filho *et al.*, 2014; 2016; Bastos-Pereira *et al.*, 2017; Taiti and Montesanto, 2020). *Cylindroniscus* presents two species occurring exclusively in Brazilian caves (Campos-Filho *et al.*, 2017; Fernandes *et al.*, 2019), also anophthalmic and devoid of body pigment. This genus has five other species for which some relationship with caves is mentioned, excepting *Cy. seurati* Arcangeli, 1929 and *Cy. yucatanensis* (Mulaik, 1960), for which the habitat is not specified (Schutz, 1970).

Fernandes *et al.* (2019) stated that *Cy. platoi* Fernandes, Campos-Filho and Bichuette, 2018 was a troglobite, since this species was found only inside caves. These authors also mentioned that the tubercles on the dorsal surface represent an adaptation to cope with high humidity of the subterranean habitats (*sensu* Schmalfuss, 1984). Moreover, they point out that this hypothesis is corroborated by the smooth surface of *Cy. seurati*, the unique epigean species known for the genus (Schutz, 1970). However, for *Pectenoniscus* all the species known until the present have such tubercles, including *P. angulatus*, the epigean representative of the genus. In this sense, depigmentation and anophthalmia cannot be considered troglomorphisms for the genus, the presence of protuberances on the body dorsal surface seems not to be associated with the restriction to the subterranean environment itself. As already suggested by Schmalfuss (1984), protuberances may be related to the highly wet condition, which is also observed in edaphic habitats. In fact, not only Styloniscidae, but also members of Trichoniscidae, in general are represented by species confined to moist environments in endogean and cave habitats (Schmidt, 2008; Tabacaru and Giurginca, 2019).

Since there are no clear differences in the morphology of epigean and hypogean species of *Pectenoniscus*, other aspects must be considered to make attempts at elucidating the ecological-evolutionary status. Endogean species present traits that converge with characters typically interpreted as troglomorphisms, such as reduction of pigmentation and ocular structures. In this sense, defining the status of such species as troglobites must be carefully analyzed. Besides the morphological similarities, endogean and strictly cavernicolous species are similar due to their requirements of habitat conditions, such as high humidity. In this sense, even endogean species tend to be found in environments with milder conditions, such as in the edaphic compartment or leaf litter of forests, since the species are highly sensitive to desiccation (Schmalfuss, 1984).

The described species, *P. montalvaniensis* n. sp. and *P. juveniliensis* n. sp. are found in caves situated in the transition between the biomes of Cerrado and Caatinga, while the other four species occur in caves inserted in the Caatinga. Caatinga represents one of the largest tropical semiarid areas in the world, which is characterized by long periods of drought throughout the year. In this biome, the dry season may last from six to eleven months, with most areas receiving less than 1,000 mm of annual rainfall, and some areas even receiving less than 500 mm annually (Nimer, 1972; 1989; IBGE, 2002). Such strong seasonality and hydric deficit culminate in a highly adapted flora, which is typically composed of deciduous forests forming sparse canopies on predominantly shallow sandy soils (Rizzini, 1979; Veloso *et al.*, 1991). Therefore, despite the fact that thorough searches for isopods were not conducted in the habitats surrounding the caves where they were found, it is plausible to assume they are restricted to the cavities considering the xeric

conditions that do not favor the establishment of epigean populations. Additionally, the here described species were strictly found in moister and deeper regions of the caves, thus reinforcing their strong hydrophilic behavior.

The species habits may also provide some indication of their restriction to the subterranean realm. Endogean species, even when found inside the caves, in general, keep their cryptobiotic habit, so that they are encountered especially under the rocks and hidden in the substrate (personal observation – RLF). Although both present preferences for wet microhabitats, the troglobites tend to be more frequently observed freely walking on speleothems or over the substrate when compared to endogean species. This has been observed for other troglobitic groups, such as the Palpigradi (Souza and Ferreira, 2019). The here described *Pectenoniscus* species were observed in such situations, freely walking in all the caves where they were collected, thus reinforcing the hypothesis that they represent troglobitic species.

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